

A TEXTBOOK OF VERTEBRATE ZOOLOGY

13TH
EDITION

Premier12

S N PRASAD
VASANTIKA KASHYAP

First edition : 1959
Thirteenth edition : 1991
Reprint : 1995

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ISBN : 0-85-226-928-5

Published by V. S. Johri for Wiley Eastern Limited
4835/24, Ansari Road, Daryaganj, New Delhi 110 002,
and printed at Ram Pratograph, Delhi

PRINTED IN INDIA

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Introduction

THE PHYLUM CHORDATA

Definition. The Chordata are animals characterised by the presence of a notochord, a dorsal gelatinous stiffening rod, present during some stage in development, tubular nerve cord, situated dorsal to the notochord and pharyngeal gill-slits.

General Characters. The Chordata include animals that can be grouped into two major subdivisions (subphyla) the **Vertebrata (Craniata)** and **Protochordata (Acraniata)**. The vertebrates are the best known and most numerous representatives of this phylum, exceeded in number of species only by arthropods and molluscs, and widely distributed in all types of habitats. The other chordates, the Acraniata, are limited to marine environments.

The **Vertebrata** are defined as animals with a backbone, but this is not exactly correct. For in the "round-mouthed" eels (Cyclostomes) including the lamprey and hagfish the axial skeleton is a cylindrical rod or cord (the **notochord**) consisting of somewhat gelatinous internal substance enclosed by a sheath of tough fibrous tissue. The notochord itself is quite unsegmented. Its fibrous sheath extends upwards on either side to enclose the dorsal nerve cord (spinal cord). In the neural arch of fibrous tissue formed in this manner minute rods or plates of cartilage are embedded. The little cartilages have been interpreted as vertebrae, but they are merely rudiments of them. Thus, here are animals without a "column", i.e., a longitudinal series of definitely formed vertebrae articulated to one another, and yet they are called vertebrates.

The fact is that the vertebral column is not the most important feature of the animals called vertebrates, it is, however, one of the characteristics of the most animals of the group. There are six fundamental characteristics of the vertebrate types and there are a few others which are also fundamental but perhaps less distinctive. This enumeration is only arbitrary, and can serve only to facilitate the work of a student. As his knowledge deepens, he will be able to free himself from the limitations which such a numerical classification may have put on his understanding.

The six most important characteristics are:

1. The pharynx and pharyngeal structures (gill-clefts, etc.).
2. The notochord or structural axis.
3. The tubular central nervous system.
4. The ventral heart.
5. Position of mouth.
6. Division of the coelom into:
 - (a) dorsal segmented part comprising cavities of the somites.
 - (b) ventral unsegmented part (splanchnocoel), which is subdivided by the transverse septum into a thoracic and an abdominal portion.

1. The **pharynx** is the cephalic portion of the digestive canal, and in all vertebrates it acquires a somewhat complicated structure. This complication depends primarily upon a series of lateral symmetrically arranged paired outgrowths from the pharynx, called **gill-pouches**. Among the lower vertebrates the number of these gill-pouches varies from five to perhaps nine pairs but in mammals there are always four distinct pairs. In the aquatic vertebrates the pouches acquire each an opening to the exterior at the side of the neck, and are then called **gill-clefts** or **branchial clefts**. The position of the clefts determines the distribution of a series of the most important cranial nerves

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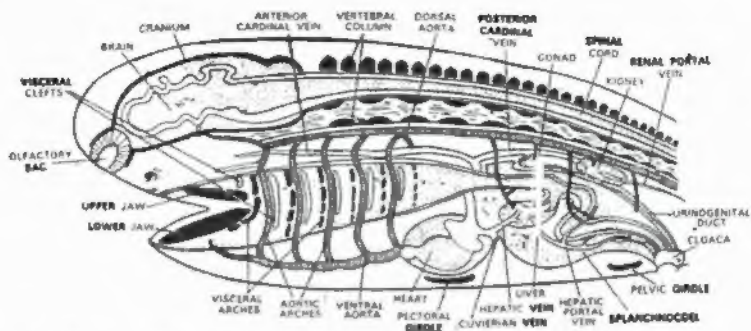


Fig. 1. Diagram showing the chief characteristics of a generalised Vertebrate, viz., the dorsal tubular nervous system; the notochord around which the vertebral column is developing; the pharyngeal gill-clefts, the ventral heart with closed blood vascular system.

and the primitive distribution of the branches of the aorta and of certain important muscles, hence the morphological features of the pharynx have a profound influence upon the entire anatomy of the body in that region. Some other important structures arise from the pharynx. From the median ventral side of the pharynx arises the thyroid gland as an outgrowth, whereas the endoderm of the third pair of gill-pouches produces the thymus and that of the fourth the parathyroids.

2. The **notochord** is a rod of vacuolated cells extending nearly the entire length of the embryo. It lies in the median plane, a little below the ventral edge of the central nervous system. It terminates in the head in the neighbourhood of the pituitary body. In some it is the only structural axis ever produced, but in the majority skeletal elements called **vertebrae** develop around the notochord. In these animals the notochord is found to run through the bodies of the vertebrae, but it diminishes as we ascend the series and in the adult mammals it persists only as a series of disconnected thickenings, the **nuclei pulposi**, of the intervertebral discs.

3. The **tubular nervous system** occurs in the chordates on the whole. In the vertebrates it is enlarged in the region of the head forming the brain. The rest of it is of smaller size and constitutes the spinal cord.

4. The **heart** is ventral in position and the flow of blood in the dorsal vessel is from the anterior to the posterior end. In higher vertebrates the heart is contained within a modified part of the coelom termed the **pericardial cavity**, the bounding wall of which forms the pericardium. In nonchordates the heart, if present, is usually a modification of the dorsal vessel, consequently dorsal in position.

5. The position of the mouth differs fundamentally from that of the invertebrates in which the brain is more or less above the mouth and the initial position of the gut is surrounded by a circumoral ring of nervous material. In the vertebrates such a ring is lacking and the entire nervous system is on one side of the body and dorsal to the mouth.

6. The body cavity in the embryo is known by the comprehensive name of the **coelom**, but it is divided into many parts. Of these there are two dorsal series, one on each side of the nervous system, which arise from cavities (**myocoel**) of what are known as the **somites** of the body. There are also two large ventral divisions which extend from the region of the head to that of the future pelvis, one division for each side of the body. These two large parts are not divided into segments at all, though the cavities of all the segments are primitively connected with these two main divisions. Comparatively early in the development of the two main cavities become connected with each other forming **splanchnocoel**, which surrounds the heart of the embryo (pericardial cavity) and extends through the future abdominal region (abdominal cavity); the two regions being separated by the **transverse septum**. It is considered to be one of the

most striking of all the morphological peculiarities by which vertebrates are distinguished from invertebrates.

Other fundamental but less distinctive characteristics include the position of the limbs, the segmented tail, the stomach, intestine and mesentery, the position of the liver and its relation to veins, the hypophysis, etc.

There are two pairs of limbs which are lateral extensions of the surface of the body and acquire an internal skeleton for support and to provide attachment to muscles. Among the invertebrates there are no structures homologous with vertebrate limbs.

The posterior part of the vertebrate body takes the form of a post-anal metamERICALLY segmented tail, which differs markedly from the unsegmented condition of the terminal portion of the invertebrate body. This tail is extremely flexible and muscular and in the aquatic forms constitutes the main propulsive organ. It is modified in various ways in the terrestrial forms and may be vestigial in the adult.

The division of the digestive tract into a stomach with gastric glands internally and intestine, and the mesentery suspending these to the dorsal wall of the abdomen is another important feature. The position of the liver, the develops as a special diverticulum of the gut, and its associated veins are equally distinctive.

The hypophysis is the embryological name applied to the structure which we know in the adult as the anterior lobe of the pituitary body. The posterior or infundibular lobe is a portion of the brain, but the anterior lobe is an outgrowth from the cavity of the mouth of the embryo. Comparatively early in the development of the individual this outgrowth becomes entirely separated from the mouth cavity and forms a closed vesicle. It exists in every known vertebrate animal, has been much studied, but still remains an organ the full significance of which is not clearly understood.

To these conceptions the student should add the following morphological notions: The vertebrate body may be defined as two tubes of epithelium, one inside the other; the outer tube (ectodermal) is very irregular in its form, and the inner tube (endodermal) is much smaller in diameter, but much longer than the outer and has a number of branches (liver, lungs, pancreas, etc.). Between these two tubes is very bulky mesoderm, which is divided by large cavities (abdominal and thoracic) into two main layers, one of which (the somatopleure) is closely associated with the epidermis and forms the body wall, and the other (splanchnopleure) joins with the endoderm to complete the walls of the splanchnic viscera. The mesoderm is permeated by two sets of cavities (i) the heart and blood vessels; (ii) the lymphatic system. It is also differentiated into numerous tissues (muscles, tendon, bone etc), organs and the internal part of the urinogenital system. The nervous system, although developed from the ectoderm, is found separated from its site of origin, and completely encased in mesoderm.

Symmetry. The vertebrates are **bilaterally symmetrical**, that is, assuming the animal to be standing on a horizontal substratum, a median vertical longitudinal plane divides the animal into right and left equivalent parts each of which is, as if, it were the mirror image of the other. Thus only one section, a vertical one in the longitudinal axis, divides the animal into symmetrical halves. There are two axes whose poles differ from each other—dorsal-ventral and anterior-posterior.

In the vertebrates the **mechanical axis** of the body is the vertebral column. In fishes and tailed amphibians, this axis lies nearly in a straight line. In land vertebrates it is more or less curved in the vertical plane, especially in the region of the head and neck. In quadruped this long axis of the body is ordinarily in horizontal position and in a biped, which assumes an erect attitude it is vertical. The quadruped walks with its head forwards and the biped erect, as such the surface which is forward during locomotion corresponds with the surface which is beneath in the quadruped.

Surfaces and Directions of the Body. With the appearance of bilateral symmetry animals usually develop the habit of keeping one particular side of the body either in contact with the substrate or facing downwards. This undersurface is the **ventral** surface of the animal while the upper surface is the **dorsal**. The forward end is **anterior**, the opposite end **posterior**, and the sides are **lateral**. The point of attachment of a structure is its **proximal** end, the free end is **distal**. Sometimes the word **cephalic** is used to denote the direction towards the head and **caudal** to denote the direction towards the tail. **Cephalad** and **caudad** are adverbial forms used for 'anteriorly' and 'posteriorly'.

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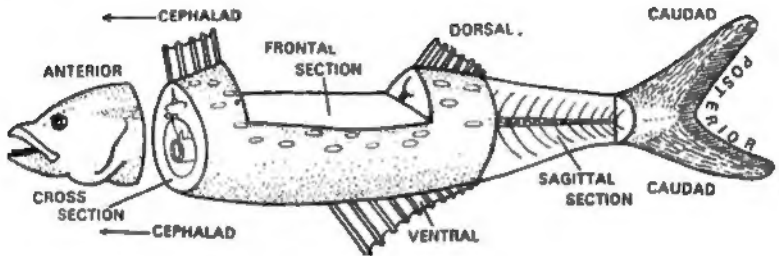


Fig. 2. Direction: planes and surfaces of a vertebrate body.

riorly' respectively.

Planes. There are three planes used as landmarks in the description of the animals. In a bilaterally symmetrical animal a cut exactly in the mid-longitudinal axis is a **sagittal section**. A **longitudinal section** on the other hand is any cut in the vertical plane parallel with the longitudinal axis. Should this pass in the mid-plane dividing it into right and left halves it becomes sagittal. Sections in the vertical plane at right angles to the long axis are **transverse** or **cross sections**. Sections in the horizontal plane are **horizontal** or **frontal sections**.

Metamerism or Segmentation. In certain animals a structural condition occurs in which all or most of the paired parts or structures are repeated at regular intervals, along the antero-posterior axis of the body. The body of such animals is made up of a longitudinal series of elements, in each of which all or most of the systems of the body are represented either by entire paired organs or structures or by a portion of the median unpaired structures. Each such division of the body is called a **metamere**, **somite** or **segment**. In some cases, such as the earthworm, the anterior and posterior boundaries of each segment may be marked externally by a constriction of the body wall, therefore, the animal is said to exhibit both **external** and **internal metamerism**. In others, however, there is no external metamerism, internal segmentation alone is present. Such animals in which various segments are nearly alike are said to display **homonomous** segmentation, but in the majority of segmented animals the various segments differ from each other in many respects, such animals are said to possess **heteronomous** segmentation. Homonomous segmentation is a primitive condition in which the various segments are more or less independent of each other and each is capable of performing all of the necessary functions of life. In heteronomous condition the segments have become unlike and there exists a division of labour among them, some segments performing some functions and others other functions. It follows therefore that in the evolution of the segmented animals there has been a continuous progression from the homonomous to the extreme heteronomous condition.

The vertebrates display heteronomous segmentation that too is internal. There is no trace of external segmentation. The vertebrates show segmentation, most clearly in the embryonic development, but it is confined to parts of muscular, skeletal and nervous systems. In the embryonic development of vertebrates the change from a somewhat homonomous condition to an extreme heteronomy can be clearly followed.

Cephalization. The segments of the anterior end of the body tend to become more and more distinctly separated from the rest of the body forming what is termed **head**. This differentiation of the head consists chiefly of the localization within the head of the main parts of the nervous system, the brain and organs of special sense. These structures control, to a very large degree, the activities and responses of the rest of the body, as such the head has become the dominant part of the organism. This localization of nervous structures and functions in the head with accompanying dominance of the head is called **cephalization**, and is more and more marked as the higher one

ascends in the animal kingdom. In the vertebrates cephalization is particularly well marked.

Cephalization is correlated with the advance of heteronomous condition. As it progresses more and more anterior segments are appropriated by the head, and in general it may be said that higher the degree of cephalization, the greater is the number of segments composing the head. In advanced cephalization, such as is possessed by the vertebrates, it is very difficult, to find out the number and boundaries of the segments actually forming the head.

VERTEBRATE ANCESTRY

During the course of organic evolution innumerable varieties of animals ranging from the simplest *Amoeba* to the most complicated forms, such as we are, have arisen, but it is not clearly understood how the vertebrates have originated. Some 550 million years back there was apparently a revolution in the general organization of the animal body with the consequent emergence of vertebrate body.

One of the earliest attempts to explain the origin of chordates was made by Etienne Geoffroy St. Hilaire (1818). According to him a vertebrate represents an insect lying on its back. If an insect turns on its back and swims naturally the ventral nerve cord becomes dorsal and the heart ventral. St. Hilaire believed that a new mouth was formed on the ventral side after the old one had degenerated. His colleague Cuvier showed that there were many notable objections to this theory. This idea of reversal of an invertebrate body was applied by many other workers with different details. Prominent workers among these were Dohrn (1875), Semper (1875-76), Minot (1897), Patten (1891-1912), Owen (1883), Gaskell (1896, 1898-1906). All these suggested that one or another type of jointed invertebrate with ventral nerve-chain and a dorsal heart was transformed into a vertebrate in which the heart is on the functionally ventral side and the nerve tube on the back. After more than a century of debate the methods remain fundamentally the same and the amount of details has become enormous. The present position is different and most of the greater phyla of typical invertebrates have been eliminated from the list of the possible ancestors of vertebrates. It is, however, necessary to sum up all these theories only because of their historic standpoint before the present solutions are discussed.

Coelenterate Theory. The three layered (triploblastic) vertebrates are supposed to have evolved from two-layered (diploblastic) coelenterates. Masterman (1897) assumed that "the bilaterality and triploid subdivision of an early embryonic stage of *Amphioxus* has been derived directly from the secondary bilaterality of a circular coelenterate, resulting from contact with the substratum and from subsequent efforts to creep forward."

Nemertean Theory. Hubrecht (1887) took the long proboscis and its sheath of the nemerteans as the primary source of the vertebrate notochord and shifted the horizontal lateral blood vessels to form the main dorsal and ventral vessels. This theory is not supported by any evidence and intermediate stages are unknown, hence it is given up.

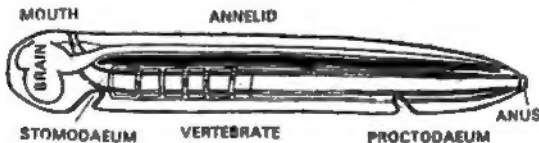


Fig. 3. Reversible diagram illustrating the Annelid theory. If the annelid is reversed the vertebrate plan will be apparent (after Wilder).

Annelid Theory. Semper (1875-76), Dohrn (1875) and Minot (1897) together with a few others suggested the possibility of annelids for being the ancestors of vertebrates. The annelids are segmented, the vertebrates are also segmented, at least as regards

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backbone, muscles and nerves, and bilaterally symmetrical as are the vertebrates. The annelid worms have a nerve cord and well-developed blood vascular system. But these present marked differences from the vertebrates as they are located in opposite positions. If, however, the annelid gets up side down (reverses) these differences can be corrected. Though reversal corrects some differences it raises some problems. For instance, the position of the mouth. In both worms and vertebrates the mouth lies on the underside, hence, it was contended that old mouth closed after reversal and the new one appeared. Then there are structures like the notochord and the gill-slits that are absent in the worms. The theory was ultimately given up.

Arachnid Theory. Some authors such as Gaskell, reasonably enough, sought the vertebrate ancestors among the arthropods. The insects and crustaceans, most numerous among arthropods, have not been given serious consideration in this case, nor have the centipedes and their relatives been considered. A more worthwhile case has been made out for arachnids, the forms that include not only the spiders, mites and scorpions but also the horse-shoe crabs *Limulus* and a number of palaeozoic relatives of this type, the eurypterids or water-scorpions. Patten devoted much of his time to the theory of vertebrate descent from the arachnid stock. The eurypterids, like other arthropods, were armoured types, with an external rather than an internal skeleton.

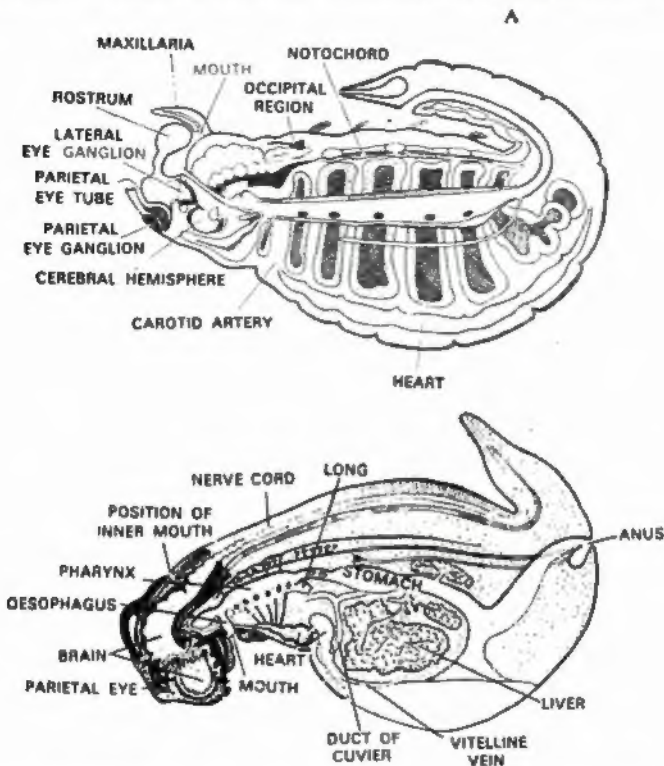


Fig. 4. A, sagittal section of a young scorpion (arachnid) which can be compared with a sagittal section of vertebrate embryo (B) (After Patten).

But some of the earlier vertebrates were also armoured and also possessed some deeper-lying skeletal structures. The fact that the eurypterid armour resembled the armour of the early vertebrates (ostracoderms) cannot be denied. The degree of likeness is often so great that it becomes a difficult task for the palaeontologist to adjudge whether a particular fossil is that of a fish or of the arthropod. Patten made ingenious use of the available palaeontologic evidence in favour of his arachnid theory. This theory emphasises that the living *Limulus* is the nearest living survivor of the invertebrate ancestors of the vertebrates.

The resemblances between *Limulus* and the larval lamprey (*Ammocoetes*) was described by Gaskell in 1908 and Patten in 1912. Remarkable is the presence of the pineal gland which is all that remains of a pair of median eyes of eurypterid ancestor of the vertebrates. One of these is still functional in the *Ammocoetes*. The ostracoderms, the earliest fossil fishes, also show two median and two lateral eyes like those of *Limulus* or allied forms. The composition of the internal cartilaginous elements of *Limulus* and *Ammocoetes* is similar. Such similarities have been traced in the case of respiratory and olfactory organs also. Gaskell's theory grew primarily out of this amazingly detailed comparison of the cranial nerves of the larval lamprey, with those of scorpions, of *Limulus* and other arthropods.

But there are numerous objections to these views. It cannot be explained as to what happened to the jointed appendages of the arthropods. There is no trace of them in the vertebrates. Further, in the above, it is the top of the vertebrate which is derived from the top of the arachnid, but here the nerve cord is on the under-side as in the annelids. If the animal is turned up-side-down then most of the resemblance is destroyed. Besides this now the anatomy of some of the oldest and seemingly most scorpion-like vertebrates is well known, and there are no features suggestive of arachnid relationship. Gaskell's *Ammocoetes-Limulus* theory was also bitterly criticized by his co-workers. Although the views of Gaskell and Patten are interesting but now they do not find any positive support. The basic designs of the two phyla are so different that a mere correspondence in either position or function between particular parts cannot be accepted as relationship.

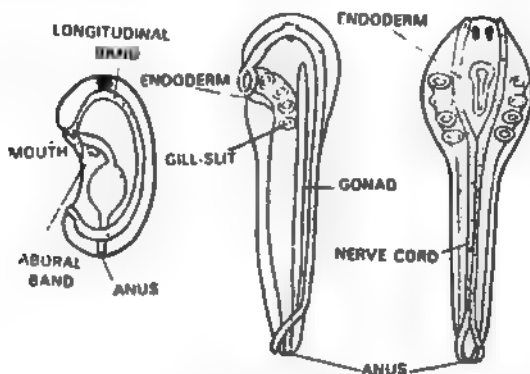


Fig. 5. Figure shows how a protochordate might have been derived from an echinoderm larva such as the auricularia (extreme right). The central figure is a protochordate (side view) and the left figure is the same dorsal view (after Garstang).

Echinoderm Theory. Some zoologists believe that the place of the ancestors of the vertebrates is among the echinoderms such as the starfishes, sea-urchins, sea-lilies and the like. No typical chordate characters are found among these radially symmetrical animals, and they have no internal skeleton and have too many peculiar and compli-

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cated organs of their own. At the first sight, therefore, this group seems to be most unpromising of all as a place for the potential ancestor of the vertebrates.

In spite of the extreme dissimilarity between the echinoderms and the chordates all these are enterocoelic type of animals. The early embryo of echinoderm is tiny free-swimming creature and floats freely in water. Unlike the adult it is bilaterally symmetrical, suggesting that the radial symmetry of the starfish is a secondary affair. This larva resembles that of the acorn worm (*Balanoglossus*) called the *Tornaria* larva. The type of development of certain of the body cavities is identical with that found in the embryos of some primitive vertebrates. What seem to be the most primitive known echinoderms, the Cambrian and Ordovician Carpoidea might be conceived tornaria-like forms which had begun to settle down to a sedentary life, acquiring an exoskeleton of many plates, together with a water pore system developed out of ciliated grooves.

Here are some positive facts and from a quarter where one would least expect them. According to Wiley "echinoderms are descended from bilaterally symmetrical pelagic ancestors represented in their development by such larval forms as the Bipinnaria and Auricularia, the general likeness between the echinoderm Auricularia and the *Tornaria* larva of *Balanoglossus* is so great that it can only be accounted for on the ground of genetic affinity. *Balanoglossus* is a protochordate supplied with gill-slits and a dorsal tubular nervous system and requires only the notochord and segmental myotomes to approximate the amphioxid type. Larval forms represent past ancestral forms, and the evolutionary sequence is worked out accordingly." The evidence from the larvae strongly suggests that in the dawn of the world, there existed some type of small, bilaterally symmetrical animal of very simple structure possessing many of the features of the larval echinoderms or acorn worm but lacking the specialization of either vertebrate group or echinoderm. By the assumption of radial symmetry and sessile mode these forms gave rise to echinoderms. But from those very forms arose types that retained their original bilateral symmetry, and which developed specialized breathing organs in the form of gill-slits, better possibilities of motility with the development of comparatively powerful musculature and a notochord for its support and better nervous control of activity through the development of a dorsal nerve cord. From this line, it is believed, the chordates appeared and these finally gave rise to the true vertebrates.

Neotenus Larva Theory Garstang (1894) was the first "to look for the trace of ancestor of the vertebrates in early instead of the adult stages of invertebrates, and he focussed his attention on the larva of Echinoderm (starfish, sea-urchins, sea-cucumbers, etc.). He showed that if the ciliated bands on the larva (auricularia) of a sea cucumber were to become accentuated and rise up as ridges leaving a groove between them, and if these ridges were to fuse, converting the groove into a tube, a structure would be produced which has all the relations of the vertebrate nervous system, including such details as the neurenteric canal," (de Beer). de Beer then points out that this view about the origin of the vertebrate nervous system has several advantages. Garstang's theory further asserts that if the larval form of such animals persisted and they became sexually mature they would provide ".... exactly the necessary material for the evolution of the chordates."

Still there are some workers who regard the similarity between the larval forms produced by similar ecological factors. H. B. Fell (1948), for instance, shows that parallelism in development has often taken place among the different subclasses of the echinoderms and he concludes that the similarity of the free-swimming larvae of certain echinoderms and (*Balanoglossus*) supplies no trustworthy evidence of common ancestry. Gregory (1951) says "We may even concede, at least provisionally, that *Balanoglossus* may not be a chordate at all and that its bag-like, ciliated, swimming larva is merely a parallel adaptation among different groups for securing a wide distribution in the search for suitable localities for the sessile or slow-moving adult."

From this it becomes apparent that no final agreement has been reached. However, there is no dispute on the point that whatever the actual type of the ancestor might have been, it must have necessarily been bilaterally symmetrical and metameric moving in a cranio-caudal direction.

N.J. Berrill (1955) in his book, "*The Origin of Vertebrates*", has suggested the following larval sequence "echinoderm-auricularia — hemichordate-tornaria protochordate-ascidian tadpole — permanently free swimming chordate. On this theory the ascidian tadpole becomes essentially an interpolation in the ascidian lifecycle, and by the suppression of metamorphosis and through further evolution it gives rise to the vertebrates as a whole. "This view finds its expression in Garstang's theory also." Berrill agrees with this view but "not with the manner in which Garstang supposes the changes to have taken place." However, this view places the ascidians in the main line of the chordate origin, at least as larvae, although not necessarily as the basic stock in other ways.

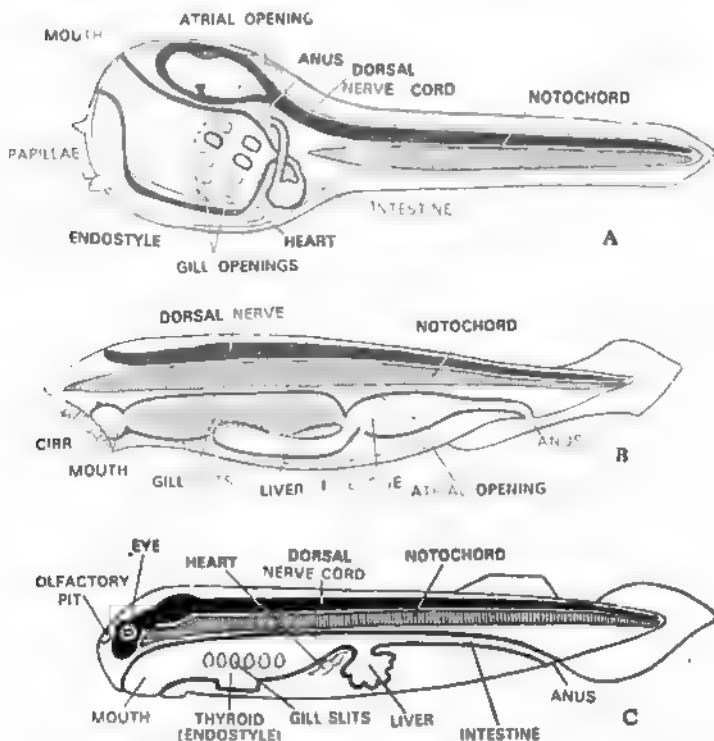


Fig. 6. A, larval urochordate; B, cephalochordate and C, vertebrate (cyclostome). The figures illustrate the transformation of an ascidian tadpole-like animal into a vertebrate

KINDS OF VERTEBRATES

All kinds of animals occur in nature without any apparent law or order. For convenience, therefore, it is necessary to invent some workable system that will group animals of similar kinds together. A regular branch of science called **Taxonomy** has evolved for this purpose. Taxonomy is the science of animal and plant classification. It is this classification or grouping of animals according to similarities, that makes

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scientific biology possible. Of equal importance in the modern biology is the attempt of the taxonomist to discover and indicate genetic relationships, similarities due to common ancestry in the course of evolution.

The working unit of the taxonomist is the *species*, usually thought of as having a real objective existence. No absolute criterion for recognizing a species as a unit has been found, however, as Darwin said, different species of animals are different kinds of animals, and it is as difficult to define kind as species. Yet certain limitations may be suggested. A group of organisms sufficiently alike to have had the same parents belong to one species, in other words, the extent of differences, morphological or physical, is within the range of individual variability. Within a species of wide geographic range the variation may be so great that the extremes would not even be considered of the same species did they not intergrade with each other. Here is another test of species. Members of the same species freely interbreed, while those of different species do not, except rarely, and therefore do not show intergrades.

Following the *Binominal system of nomenclature*, the general adoption of which dates from the work of Carolus Linnaeus (18th century), each organism is known by two names, (i) the name of *genus* to which it belongs, always, written with the initial letter capitalized; and (ii) the name of the *species*, its initial letter never capitalized. These two names constitute the *scientific names*. Now it is customary to print scientific names in italics. The names are of Latin form because when the system was adopted Latin was the international language of the scientists and since it is now a "dead" language its forms are not subject to change.

Categories of Classification. The species is the smallest category in classification. Species form a *genus*, genera a *family*, families an *order*, orders a *class* and the classes are combined into *phyla*. Several intermediate steps in classification are inserted to clarify the complexities of animal or plant relationships. The class may be divided into *sub-classes*, each containing several orders, or a family with other families may constitute a *superfamily*. An order may contain more than one superfamily. The criteria of other intermediate steps (such as *superorder*, *infraclass*, etc.) are not established. These puzzle even experts, as much a beginner in taxonomy need not know all these details.

Rules of Nomenclature. There are numerous varieties of animals and many persons are engaged in taxonomic work. As such there is every possibility of some confusion in nomenclature. Such a confusion did occur in the past. The same name has been given to different animals and different names have been given to the same animal. Linnaeus used some rules of nomenclature and some were proposed later. The International Congress of Zoologists in 1898 appointed a permanent commission to prepare an International Code of Nomenclature and to give decisions on difficult cases. The following are some important provisions of the code.

(1) Zoological and botanical names are distinct (the same genus and species name may be used, but is not recommended for both, as animal and a plant); (2) no two genera in the Animal Kingdom may bear the same name; (3) no names are recognized prior to those included by Linnaeus in the "Systema Naturae" tenth edition, 1758; (4) scientific names must be either Latin or latinized and preferably printed in italics; (5) the genus' name should be a single word (nominative singular) and begin with a capital letter; (6) the species' name should be a single or compound word beginning with a small letter (usually an adjective agreeing grammatically with the genus' name); (7) the author of a scientific name is the person who first publishes it in a generally accessible book or periodical, with a recognizable description of the animal; (8) when a new genus is proposed the type species should be indicated; (9) a family name is formed by adding *IDAE* to the stem of the name of the type genus, and a subfamily name by *INAE*.

From an embryological point of view the vertebrates may be separated into two main divisions, the *Amniota* and the *Anamniota*, distinguished by the presence or absence of the *amnion*, a thin membrane that surrounds the early embryo. It occurs in reptiles, birds and mammals which together constitute the *Amniota*; and is absent in the fishes and amphibians which are called the *Anamniota*. These two divisions are also distinguished by other peculiarities. The higher forms referred to above, have an

organ known as **allantois**, an appendage of the embryonic gut, which is lacking in the lower forms. The comparative anatomist finds many points of resemblance between the various classes of fishes on the one hand, and the Amphibia on the other, and indicates this relationship by the use of the term **Ichthyopsida** ("fish-like" animals). In our present classification the term **Ichthyopsida** is synonymous with **Anamniota**. The comparative anatomist further recognizes a close relationship between birds and reptiles, and puts these together under **Sauropsida** ("reptile-like" animals).

The following are the generally accepted categories of classification:

Kingdom
 Phylum
 Subphylum
 Superclass
 Class
 Subclass
 Cohort
 Superorder
 Order
 Suborder
 Superfamily (-oides)
 Family (-idae)
 Subfamily (-inae)
 Tribe (-ini)
 Genus
 Subgenus
 Species
 Subspecies

The system of classification of the Chordata used in the present book is summarised in the chart given on the next page. The detailed classification of the different classes has been given after the description of the types of each class.

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Phylum CHORDATA

Chordates with cranium or brain box, etc

Subphylum VERTEBRATA

Cranates with visceral arches and vertebra, column

Subphyla

Main characteristics of Classes

HEMICHORDATA.

Notochord anterior, short, nerve tissue in epidermis.

ENTEROPNEUSTA. Tongue worms, Wormlike hemichordata with many gill-slits.

PTEROBRANCHIA. Minute; gill-slits two or none.

TUNICATA. Adults contained in secreted tunic, notochord and nerve cord only in larva.

LARVACEA. Tadpole-like minute Tunicata with two gill-slits and temporary tunic.

ASCIDIACEA. Tunicata with many gill-slits and the tunic with scattered muscles. Ascidians.

THALIACEA. Tunicata in which the tunic is provided with circular muscles. Chain tunicates.

CEPHALOCHORDATA.

Notochord and nerve cord extend along entire body and persistent, as are the gill-slits.

LEPTOCARDI. Lancelets. Slender, fishlike segmented Cephalochordata in which the epidermis is one layered, many gill-slits occur and there are no scales.

Superclass

AGNATHA

Vertebrates without true jaws or appendages.

***OSTRACODERMI.** Ancient armoured fishes, scales large often fused as cephalothoracic shield.

CYCLOSTOMATA. Skin without scales, mouth rictorial; gill-slits 6 to 14. Cyclostomes.

Superclass

GNATHOSTOMATA.

Vertebrates with jaws and usually with paired appendages.

***PLACODERMI.** Ancient fishes with primitive jaws and complete gill-slits before hyoid.

ELASMOBRANCHII. (CHONDRICHTHYES). Skin with placoid scales; cartilaginous skeleton and 5 to 7 pairs of gills in separate clefts. Sharks and rays.

ACTINOPTERYGII (OSTEICHTHYES). Skin with cycloid or ctenoid scales; bony skeleton and 4 pairs of gills in a common cavity under opercula. Bony fishes.

CHOANICHTHYES. Nostrils connecting to mouth cavity; each paired fin with large median lobe (sometimes cross joined) and dermal fin rays along side. Lung fishes.

AMPHIBIA. Skin moist, soft no external scales. Amphibians.

REPTILIA. Skin dry with scales or scutes. Reptiles.

AVES. Skin with feather; fore-limbs modified to form wings; warm-blooded. Birds

MAMMALIA. Skin with hair, warm blooded and suckle young.

Part One

THE PROTOCHORDATES

1. The Protochordata

The **Protochordata** or **Prochorda** are simpler forms of the chordate animals in which the notochord is wholly or partially formed and the vertebral column and skull are lacking (hence *Acrania*). This division includes a heterogeneous (polyphyletic) group of animals of the phylum **Chordata**, most of which are fairly related to the vertebrates but none possesses the full complement of vertebrate characters.

The Protochordata are divided into two classes: (i) the **Tunicata** (or **Urochordata**) or ascidians which in the adult forms are entirely different from the vertebrates, and (ii) the **Cephalochordata**, a group containing various species of *Amphioxus* (-*Branchiostomum*), a small animal, which looks fish-like, but has no fish-like skeleton, brain or eyes. A third group, the **Hemichordata**, was formerly included among the Protochordata. It comprises worm-like forms, whose vertebrate affinities are much more remote. Bateson (1885) included the Hemichordata in the phylum Chordata, a classification that has largely been followed in Zoology texts up to now. In many elementary books this practice still continues. But many French and German authors have unequivocally rejected this view. Hyman (1959) has separated this from chordates and placed it along with enterocoelous coelomates between Chaetognatha and Progonophora. In the present book the Hemichordata is being described as an appendix to the Protochordata.

The present system of the classes of the protochordates is different. As is evident from the above the hemichordates, represented by the pterobranchs and enteropneusts, occupy a controversial position and exhibit no more than a convergent resemblance to chordate organization. *Amphioxus*, on the other hand, is a degenerate form, and is not a satisfactory vertebrate prototype. Ascidians, through their larval forms, then constitute the actual stock from which the chordates have emerged. Therefore, ascidians are being described first and *Amphioxus* following that. Although it is now, more or less, established that the hemichordates have no real relation with chordates, yet they are being described as an appendix to the Protochordata.

THE TUNICATA (UROCHORDATA)

Definition. The Tunicata (or Urochordata) are hermaphrodite marine chordate animals, contained in secreted tunic in adult stage, which are usually sessile and degenerate, and may be solitary or colonial, fixed or free, the chordate characters in these are well represented in their larval stage in which the notochord is restricted to the posterior part of the body (tail).

General Remarks. The Urochordata (Gr *uro*, tail) are marine animals found practically in all parts of the sea, and at all depths. They extend from the Arctic and Antarctic regions to the tropical waters and from the littoral zone down to the abyssal depth of over three miles. In these peculiar ciliary-feeding animals the chordate character is lost in the adult. For this reason they had varied history. They were included with the invertebrates such as the Polyzoa and Brachiopoda by early writers. Historically speaking the ascidians are quite old known animals. Aristotle was the first to describe a simple ascidian calling it *Tethyum* more than two thousand years ago. The real advance in the study of this group, however, was made after the description of *Botryllus*¹ a compound ascidian. On the basis of the study of Cuvier (1815) on simple

¹ Schlosser and Ellis (1756) in the *Philosophical Transactions of the Royal Society*.

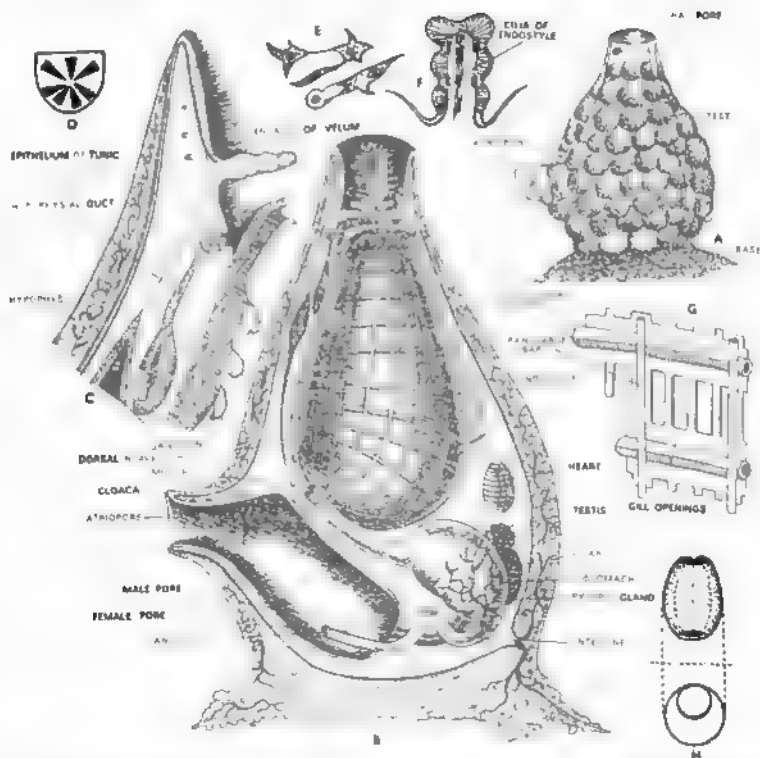


Fig. 1.1 Anatomy of an ascidian. A, entire animal, B, diagrammatic sagittal section, C, anterior portion enlarged to show oral tentacle and hypopharynx and D, transverse section of a muscle (after Maurice), E, Test cells, F, endostyle G, pharyngeal wall H, heart, surface view and section.

ascidians and Savigny (1815) on compound ascidians. Lamarck (1816) created the class *Tunicata*, including, besides the simple and compound ascidians, the pelagic forms *Pyrosoma* and *Salpa*. Carl Schmidt (1845) discovered the presence of "tunicin" a substance similar to cellulose. Others who contributed to the study of ascidians include Huxley (1851), Gegenbaur, Vogt, H. Muller, Krohn, Leuckart, H. Milne, Edwards, Herdman, Metcalf, Minot, Bateson, Garstang and recently Brien (1930) and Berrill (1951), etc.

Ascidians were formerly regarded a degenerate offshoot of the vertebrates but now they are regarded as primitive stock from which the vertebrates have arisen. If the ascidians "represent the stock from which the vertebrates and other chordates evolved, the events we are concerned with occurred no later than Cambrian times and in all probability at a much earlier period. Accordingly, the original ascidian stock has had 500 million or more in which to evolve, differentiate, and increase in size, all the time retaining the ascidian tadpole as a larval form. During such an eternity, which embraces the entire period of vertebrate evolution from the formation of the first free-swimming adult chordate to the present remarkable exhibition of vertebrate behaviour, the ascidians as a group have had ample opportunity to acquire specialization which confuse the picture" (Berrill).

TYPE ASCIDIAN

The most common ascidian inhabiting the Indian seas is *Herdmania*.¹ Only three species of this genus have been recorded from the Indian Ocean of which *H. pallida* and *H. ceylonica* occur in the coastal waters and *H. mauritiana* has been found from deep seas. The description given in the following pages is of a typical ascidian from which *Herdmania* does not differ much. The differences that merit attention have been recorded.

The ascidians are attached, to the substratum usually separately by means of 'foot' (Fig. 1.2), which may be expanded and elongated in case the substratum is sandy. The "foot" is also known to act as a balancer in case the animal is detached from the substratum rather accidentally, and keeps it erect. The foot may be replaced by a flat or concave disc if the animal is attached to hard substratum such as a rock or a mollusc-shell. At the distal end there are two openings, the branchial or oral pore and the atrial pore. These pores are situated on short protuberances of the body called branchial and atrial siphons. When disturbed in the living state the animal can emit jets of water with considerable force (hence the common name "sea-squirt"). The branchial aperture opens on the morphological anterior end and is surrounded by eight lobes (lips), whereas atrial aperture is on the dorsal edge from one-third to one-half way down the body (shown much below in the figure 1.1 redrawn after Delage and Herouard) and is guarded by six lobes. In *Herdmania* the two apertures are more or less at the same level and are guarded by four lobes in each case (Fig. 1.2).

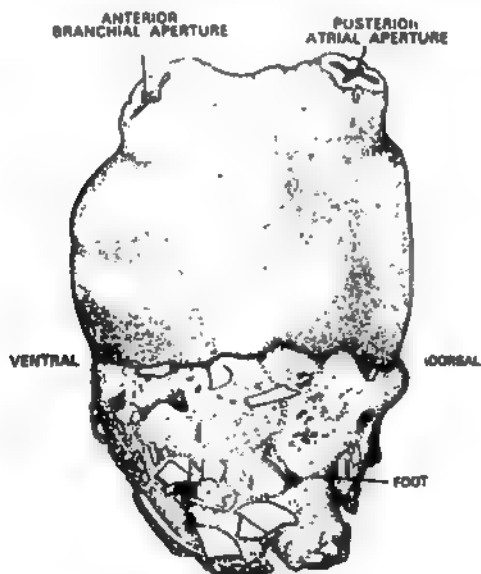


Fig. 1.2. *Herdmania* from life (after S. M. Das).

¹ Described by S. M. Das, D. Sc. as one of the Indian animal types, published in the series, "The Indian Zoological Memoirs" in 1936.

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The entire body is covered by a tough cuticular covering [called 'tunic' or "test" of dull grey colour. Fresh specimens of *Herdmania* appear pink. The reddish tint is because of scattered areas of blood capillaries and bright red vascular ampullae in the surface layer of the test. The bright red colour of the ampullae is due to the presence of red pigment in their walls.

The size and shape of ascidians is varied. Some are small and microscopic, whereas, others are about a foot in diameter. *Herdmania*¹ is about 9 to 13 cm. long, 7 cm. broad and 4 cm. thick. So far as the shape is concerned no two animals are absolutely alike. Some may be pearshaped, some may be oval and some may be even oblong (*Herdmania*).

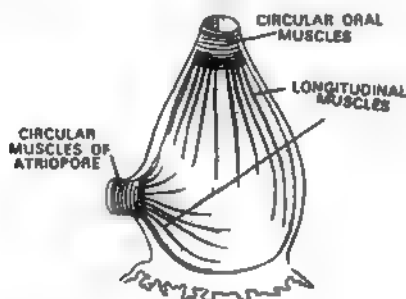


Fig. 1.3. Figure showing the arrangement of muscles at the openings of an ascidian.

Test. The test is soft and leathery protective covering of the body. In young animals it is more or less transparent, but becomes opaque in older forms due to thickness and also because some external material becomes associated with it. It is quite a notable structure as it contains a substance called tunicine which resembles cellulose in composition and behaviour under treatment with various reagents. It is cartilaginous in appearance and consistency and cuts like cartilage. Its inner surface is smooth and glistening interrupted by projections from partially embedded spicules. The test is responsible for the definite form of the animal and forms the foot at the postero-ventral region. In a living animal the test is continually worn out at the surface.

Histologically the structure of the test consists of a clear matrix (wavy or fibrillated in some cases) in which are embedded many corpuscles or cells of different types, interlacing fibrils and spicules, etc. It is the matrix that contains the cellulose-like tunicine, which may form over sixty per cent by weight of the entire test. Morphologically the test is a cuticle being secreted by the outer surface of the ectoderm and the cells it contains have migrated to it from the body. Many of these cells are mesodermal. Six different types of cells have been reported: (i) Large spherical or ovoid cells staining easily in eosin hence called eosinophilous cells, (ii) amoeboid cell, smaller than the eosinophilous cells, are few and far between (iii) numerous small eosinophilous cells, each with excentric nucleus, scattered throughout, (iv) spherical vacuolated cells are rounded cells filled with small or large number of vacuoles, (v) granular cells lie near the surface of the test, (vi) small nerve cells, each giving out two to six processes and containing a large nucleus. The processes are continued into nerve-fibrils which traverse the substance of the test and connect the various nerve-cells. In the test of *Asicida* large bladder cells occur. They do not seem to occur in *Herdmania* or else they are modified in any of the above variety. In some of the Tunicata the test-cells produce spicules of various shapes.

¹ Reported by S. M. Das, 1936.

A characteristic of the test is the presence of the test-vessels. These are out-growths of the body wall covered by ectoderm and containing prolongations of the blood channels from the connective tissue of the body wall (mantle). The test-vessels in *Herdmania* end in large rounded or ovoid vesicles, the terminal knobs or vascular ampullae, each of which is surrounded by a layer of red pigment cells, which form the characteristic red patches of the test. The cells surrounding the ampullae are ectodermal and are richly supplied with nerve-fibres. They thus form tactile centres near the external surface of the test. The test-vessels carry nourishment to the test along with the blood flowing in the blood vessels of the interior. Besides, they form accessory respiratory apparatus. In some (Botryllidae) the terminal knobs pulsate and aid in keeping up the circulation. The test-vessels are much enlarged and branched in the foot.

Spicules. Two types of calcareous spicules are found in the body, small *microscleres* and large *megasccleres*. The microscleres occur scattered only in the test. Each spicule has a rounded nearly smooth head at one end and tapers to a point at the other. The body of the spicule bears five to twenty rings of spines, the large ones being nearer the head and the smaller ones away from it. The megasccleres are either spindle-shaped or pipette-shaped. The spindle-shaped ones vary from 1.5 mm. to 2.5 mm. in size, have rings (20-60) of spines all over the body and are enclosed in connective tissue sheaths. They lie scattered throughout the body in most of the tissues. In posterior half of the test they are regularly arranged and form a sheath round the vessels traversing the test. They are abundant in the mantle but are not distributed uniformly, and are usually arranged in linear rows in sheaths. In the region of the stomach, the gonads and at the bases of the siphons they form dense accumulations but are sparse at the base of the longitudinal muscles. The pipette-shaped spicules are larger up to 3.5 mm. long having a large spherical swelling in the middle, giving it the shape of a pipette. Often the spicules are U- or V-shaped, not straight. They are also covered with rings of spines and are lodged in connective tissue sheaths. They occur in abundance in the mantle, specially in the region of the gonads and the lobes of the liver. The function of the spicules is perhaps to keep the test firmly attached to the mantle. Smaller spicules that surround the blood vessels do so to stiffen the walls of the vessels.

Body wall. The body wall or mantle lies within the test, interrupted only at the branchial and atrial apertures, and consists largely of parietal mesoderm with blood sinuses and muscle bundles running circularly, longitudinally and obliquely, enclosed between an outer and an inner layer of ectoderm.

The outer ectoderm is a simple epithelial layer made up of flattened cells more or less hexagonal in outline. It is turned in for a short distance at the branchial aperture (mouth) and atrial aperture (cloaca), as a short stomodaeum and proctodaeum respectively, lined in each case with a delicate prolongation of the test. The ectoderm has been reported to contain bright red, yellow and opaque white pigment cells in different regions.

The next layer, the parietal mesoderm, is largely formed of connective tissue, both homogeneous and fibrous, with cells, blood sinuses and innervated by a few nerve fibres. The muscles are all formed of very long fusiform non-striped fibres and are restricted to the antero-dorsal half of the body, the postero-ventral part being without muscles. The muscles are reddish in the living state. In correlation to the sessile habits the muscles are not well developed here except those connected with the branchial and atrial aperture in order to help squirting of sea-water. For this purpose three groups of muscles have been distinguished, the branchial group comprising the circularly disposed annular set and a longitudinal set at the branchial the atrial group comprising an annular set and a longitudinal set at the atrial aperture, and the branchioatrial group comprising muscles running between the branchial and atrial apertures. Of the latter there are two pairs of muscles in the region of the neural gland and one deeper extending along the dorsal ridge of the branchial sac. The circular muscles bring about the contraction of the siphons while the general contraction of the body is brought about by the longitudinal muscles.

The connective tissue cells are of various types, chiefly amoeboid and vacuolated. They migrate into the test through the ectoderm and secrete matrix. The inner ectoderm forms the lining of atrial cavity. It has been called the third tunic by some

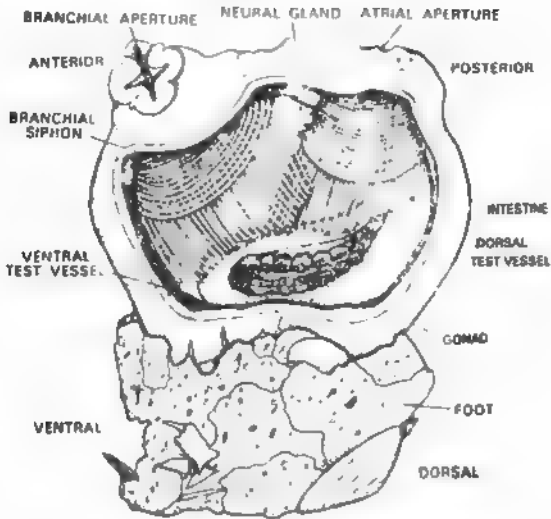


Fig. 1.4. *Herdmania* test open on one side to expose internal structure (after S. M. Das).

older writers who prefer to call the test and the parietal mesoderm as the **first** and **second mesoderm**. But as it is ectodermal in origin consisting of more or less flattened cells it has here been called the **inner ectoderm**.

Cavities of the Body. The mantle encloses a large atrial or peribranchial cavity which opens to the exterior dorsally by the atrial aperture. Before opening it forms the cloaca along the dorsal edge of the body. At the anterior and ventral region, the wall of the branchial sac is fused with the mantle, with the result that the atrial cavity is separated into right and left halves which, however, are continuous dorsally and lead into the cloaca. Thus the atrial cavity surrounds the branchial sac with which it communicates by the **secondary gill-slits** or **stigmata**. At the antero-dorsal end the mantle forms two well-marked **siphons** or short wide tubes which lead from branchial and atrial apertures. Each is surrounded by strong sphincter muscles and lined by invaginated ectoderm and test. The one leads into the branchial sac or modified coelom and the other into the atrial cavity.

Coelom. There is no extensive body cavity lodging the viscera as in the vertebrates. The true coelom formed in the mesoderm is very much suppressed, as a result of the encroachment of the atrium, and is represented in the adult by pericardium and by small cavities in the renal and reproductive organs and ducts. These questionable coelomic structures are only indirectly derived from the archenteron. They do not arise as paired hollow pouches, but as a pair of originally solid mesodermal plates. This great reduction of the coelom or its complete absence, as some authors believe, has been regarded as a result of degeneracy. The mesoderm does not show any tendency toward metameric segmentation at any time.

Alimentary Canal. The alimentary canal comprises a narrow tubular **buccal cavity** or **branchial siphon**, a large modified **pharynx** or **branchial sac**, a short **oesophagus**, **stomach**, **intestine** and **rectum** that finally opens into the atrial cavity. Two-lobed liver and the pyloric gland serve as glands associated with digestion.

The branchial aperture opens into the branchial siphon (buccal cavity) which is stomodaeal in nature being lined by an inpushing of the outer epidermis. At the base of

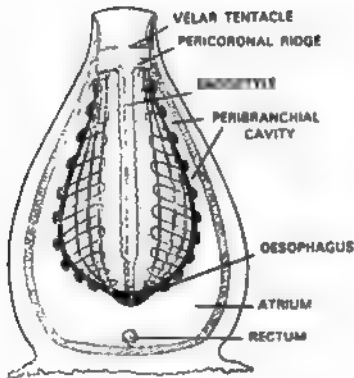


Fig. 1.5. Diagrammatic sketch showing the position of the endostyle and its relation to other structures.



Fig. 1.6. Side view of a tentacle (highly magnified) (after S. M. Das).

the siphon, just about the line of junction of the ectoderm of the stomodaeum and endoderm of the mesenteron, is placed a circle of simple hair-like **tentacles**, which stand out at right angles to the wall and more or less completely meet in the centre to form a delicate sensory sieve through which all the water entering the body has to pass. These tentacles not only act mechanically as strainer, but are also sensitive, although only scattered sensory cells occur on them. Only microscopic food particles are allowed to pass into the pharynx, coarser particles being held up. The tentacles are of different sizes. In *Herdmania* four size groups occur (8 to 10 about 5 mm. in length; 8 to 10 about half this size and alternating with them; about 16 smaller about 1.5 mm. in length placed alternately between large and medium-sized tentacles and about 32 very small about 0.5 mm. in length. Each tentacle is a curved sickle-shaped structure bearing a large number of paired lateral branches (pinnate). It is attached to the wall by a broad base (Fig. 1.6). Each consists of a covering of a single layer of small epithelial cells enclosing a connective tissue core interspersed with blood-sinuses and innervated with nerve fibres.

Behind the tentacles lies the plain or papillated **prebranchial zone**, bounded behind by a pair of parallel and closely placed ciliated ridges, the **peripharyngeal bands**, separated by a **peripharyngeal groove**. The peripharyngeal bands encircle the anterior end of the branchial sac. The anterior band forms a complete ciliated ring while the posterior band is interrupted dorsally and ventrally, the interrupted ends being continuous with the **dorsal lamina** in the mid-dorsal line and with the **endostyle** in the mid-ventral line. In front of the junction of the posterior peripharyngeal band and the dorsal lamina lies a swollen hemispherical, **dorsal tubercle**. Each peripharyngeal band consists of tall columnar cells enclosing a central connective tissue core filled with blood sinuses.

The **branchial sac** is the largest part of the body extending almost up to its posterior end, while the rest of the alimentary canal lies on its left side. The branchial sac communicates with the atrial cavity by a large number of apertures, the **stigmata**. The roof of the sac is formed by a ridge, the **dorsal lamina**, and on the floor lies the **endostyle** or the **hypobranchial groove**. In many ascidians the inner wall of the branchial sac is raised into a number of broad longitudinal folds thus increasing the surface that comes in contact with the sea-water. The number of the folds is variable,

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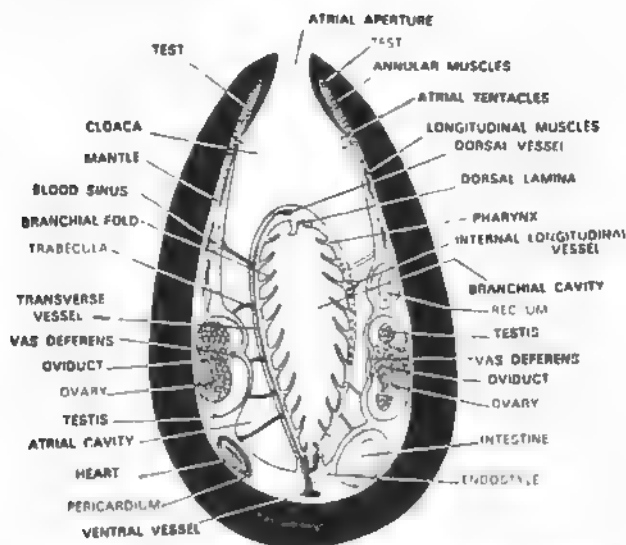


Fig. 1.7. Diagrammatic transverse section of the animal through the atrial siphon.

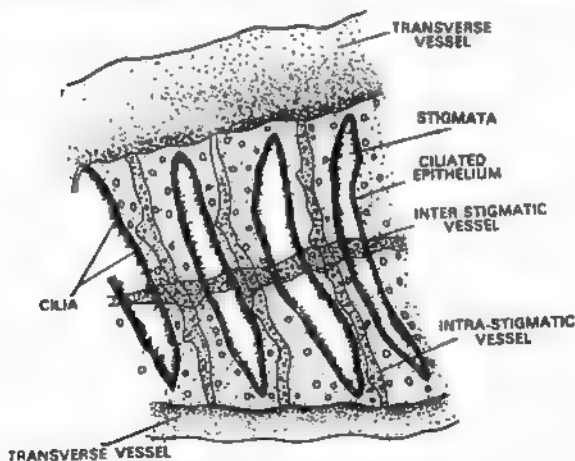


Fig. 1.8. A few stigmata enlarged to show ciliation (after S.M. Das)

generally ten. Externally the branchial sac shows a number of squarish depressions at the bases of these longitudinal folds, as the branchial wall here gets invaginated. The branchial sac has a rich blood supply. A set of blood vessels runs along the inner surface of the sac and along the folds. These have been called the **internal longitudinal vessels**. Externally the branchial sac bears a large number of large and small promi-

nent external transverse vessels. The transverse and longitudinal vessels cross one another at right angles and enclose more or less rectangular areas of the branchial wall bearing many stigmata. There are about 10,000 square areas each bearing about 20 stigmata giving rise to about 200,000 stigmata on each of the branchial sac. The stigmata are bounded by cubical or columnar epithelial cells which are ciliated. The cilia keep on beating constantly giving rise to water current streaming through the body.

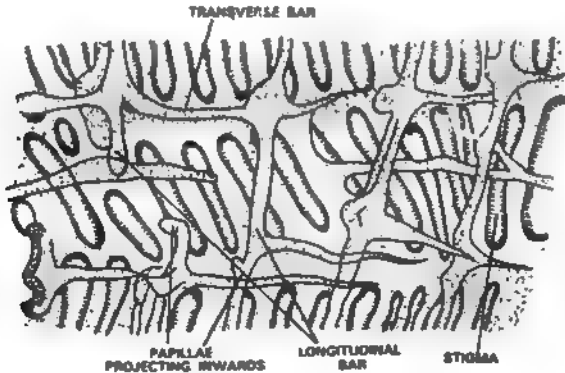


Fig. 1.9. A portion of the branchial wall of *Ascidella scabra*.

Endostyle. The food particles consisting of microscopic plants and animals are carried in through the branchial aperture by the water current but they do not pass out to the atrium. Most of them are entangled in the viscid mucous which passes by ciliary action along the groove between the peripharyngeal bands. This mucous is secreted by a long glandular ciliated canal, the endostyle¹ or hypobranchial groove, which runs along the entire ventral edge of the branchial sac and measures about 8 centimeters in *Herdmania*. The sides and especially the floor of the endostyle, are richly ciliated, the cilia of the floor being long looking like a tuft of flagella. On the sides there are four (or six) strongly marked, peculiarly shaped granular tracts two (or three) on each side, running along its length and separated by areas of closely packed fusiform cells with short cilia amongst which are found some bipolar sensory cells.

The dorsal lamina is a more or less ridged or corrugated fold in the short mid-dorsal region. On the free edge it may be armed with marginal tags or even larger tentacle-like processes called the dorsal languets (Fig. 1.10), numbering from 20 to 30 (in *Herdmania*). Usually they are short and conical covered by non-ciliated epithelium enclosing a connective tissue core filled with blood sinuses. In the living state the free edge of the lamina is curved to the right (Fig. 1.7) forming a fairly perfect tube along which the train of food passes.

The mucous secreted by the endostyle forms a cord and is carried forward by the action of the large cilia at the floor of the endostyle to the groove between the peripharyngeal bands and after encircling the anterior end of the branchial sac and collecting food particles it passes backwards along the dorsal edge of the branchial sac to the oesophagus guided by the dorsal lamina. In some cases the single mucous cord breaks up into two cords at the anterior end, each passes round the prebranchial zone

¹According to Muller this structure corresponds to the hypobranchial groove of *Amphioxus* and the thyroid gland of vertebrates.



Fig. 1.10. Side view of a part of the dorsal lamina (after S. M. Das).

of the pharynx, collects food particles and in the mid-dorsal region the cords reunite to form a single cord that passes in with food particles.

Orton¹ has observed that the mucous is not carried forward along the groove as was believed formerly but is lashed out of the groove in a transverse direction by its two pairs of lateral rows of cilia. He has further shown that the food particles are drawn in along with the water current, then pass through the branchial tentacles and the peripharyngeal band and settle down on the pharyngeal wall. They are not carried along the endostyle, but are caught in the mucous that passes across the endostyle and are gradually transported across the inner wall of the branchial sac to the dorsal lamina where they are rolled with the mucous into a cylindrical mass which is carried backward in the oesophageal opening.

The oesophagus leaves the branchial sac in the dorsal middle line, near the posterior end of the dorsal lamina. The posterior most part of the branchial sac from which the oesophagus arises is known as the oesophageal area. It is around this area that all the folds of the branchial sac converge, and moreover this area is without longitudinal and transverse vessels and also stigmata, characteristics of the branchial sac. The opening of the oesophagus is guarded by two large lips, the right and left. The oesophagus is a short curved tube which leads ventrally to the large fusiform, thick walled stomach. The oesophagus is a thick walled tube; having four ciliated grooves internally, which direct the food-laden mucous thread into the stomach.

The inner epithelium of the oesophagus is ciliated. In some (*Ciona*) it also possesses mucous glands.

The stomach is comparatively larger sac but with thinner walls which are smooth internally except where the liver ducts open into it. The ramifications of the pyloric gland are visible throughout, notably prominent in the distal half. A single layered glandular epithelium of tall cell forms the lining of the stomach. The cells contain four to six bladder-like bodies filled with gastric secretion. The wall further shows sections of the ramification of the pyloric gland. The stomach passes directly into the intestine ventrally. On emerging the intestine turns anteriorly then dorsally and then posteriorly, thus forming a loop, the **intestinal loop**, open towards the posterior side. This loop lodges the left gonad. Now the intestine again turns anteriorly and then runs straight as the rectum thus forming a second loop, the **rectal loop** (Fig. 1.20), which is open toward the anterior side. This loop lodges the renal vesicles. The wall of the intestine is thinner than that of the stomach and is lined internally with a single layer of tall columnar cells. The wall is thickened to form a **typhlosole**, a pad which runs along its entire length, so as to reduce the lumen of the tube to a crescentic slit. No typhlosole has been reported in *Herdmania*. The rest of the intestinal wall is made up of loose connective tissue enclosing large blood sinuses. The rectum curves slightly towards the dorsal side and opens in to the cloaca at the anus situated near the atrial opening. The anus is guarded by four moderately thick lips (*Herdmania*). The lining of rectum consists of flagellated columnar epithelium which extends on the anal lips. The connective tissue wall of the rectum encloses blood sinuses as in the intestine.

¹ Journ. Mar. Biol. Ass. Vol. 1913. 1.

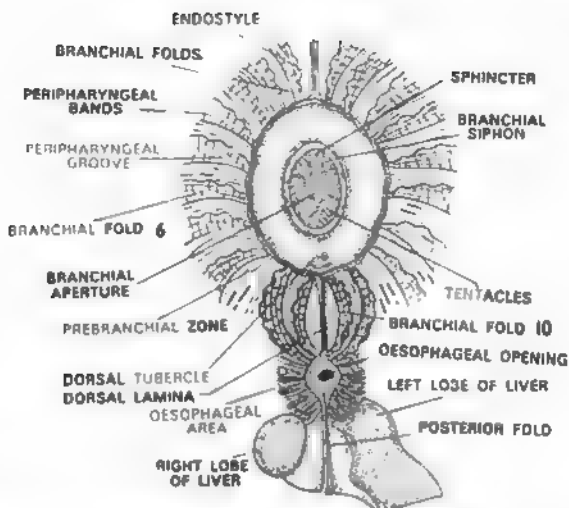


Fig. 1.11. Diagram showing the relation of the branchial folds, peri-pharyngeal bands, dorsal lamina, oesophageal area and endostyle (after S. M. Das).

The "liver" is the name given to two large chocolate-coloured digestive glands lying against the stomach. In *Ascidia* no separate gland of this type is found but in other Tunicata including *Herdmania* a gland exists and functions more or less like liver. In *Herdmania* the left lobe is a large gland attached to the wall of the stomach facing the left side of the branchial sac and obliterating the stomach from view. The left lobe is about one third of the right one and extends across the mid-ventral of the branchial sac towards its right side. The liver appears papillated in general appearance. It is made up of a large number of branched tubules embedded in a connective tissue matrix containing blood sinuses. The hepatic tubules, as they may be called are arranged in radial groups around each of the ducts of the liver that open into the stomach. The tubules are made up of single-layered granular epithelium with thin basement membrane. The space between the tubules is filled with loose connective tissue. In

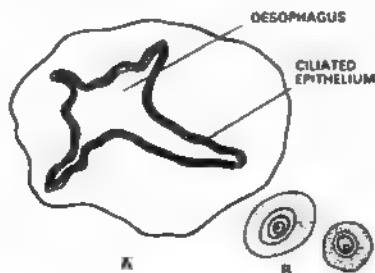


Fig. 1.12. Diagrammatic transverse section of the oesophagus (A); and starch granules (B) found in the walls of oesophagus stomach and liver

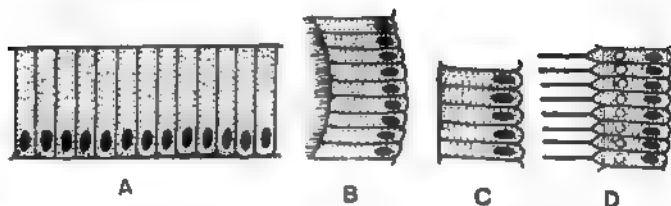


Fig. 1.13. Epithelial cell lining the stomach (A), liver duct (B), intestine (C) and rectum (D) after S. M. Das

Tethyum pyriforme Berrill has described three kinds of epithelial cells in the liver, secretory, ciliated and absorptive. The cytoplasm of all these is more or less homogeneous. The ducts of the liver open in three main longitudinal depressions on the internal surface of the wall of the stomach facing the liver.

The pyloric gland is a system of delicate much branched tubules which ramify into the walls of the stomach and intestine, mostly parallel to their surface and send their dilated ends (ampullae) towards the inner epithelial lining of the intestine. These tubules lead into a number of ducts which join together at the beginning of the intestine to open into it by a single opening on the branchial face almost in the middle of the first intestinal loop. The pyloric tubules have a single layered lining made up of small cells, whereas the ampullae have polygonal granular cells lining it. In some (Cynthiinae) the pyloric gland opens into a special chamber called the pylorus which is not found in *Herdmania*. The pyloric gland probably functions as pancreas and as an excretory organ also.

Physiology of Digestion. Yonge (1925) working on *Ciona intestinalis* concluded that the oesophagus possesses ciliary epithelium, also mucous glands and conducts the food to the stomach, the cells of which probably secrete digestive enzymes but no mucous. The hind-gut again contains only mucous secreting cells and numerous glycogen storing cells which are also present in the stomach sometimes. Glycogen occurs throughout the gut, exception being the oesophagus, the branchial sac and the ovary. Digestion takes place primarily in the mid-gut, to a smaller extent in the

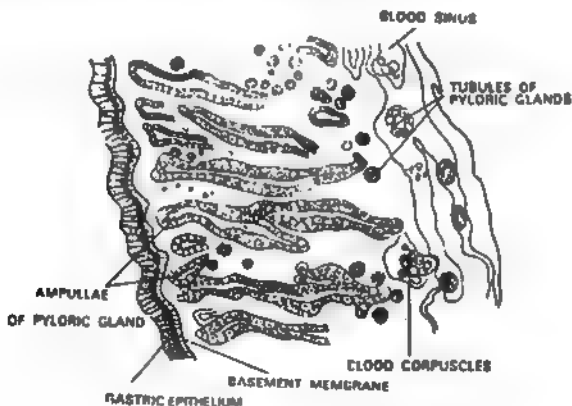


Fig. 1.14. Transverse section of the stomach (after S. M. Das).

stomach and very slightly in the hindgut. *Ciona* has no well-defined liver. Its function, however, has been studied by Berrill (1929) in *Tethyum pyriforme* and by Das (1936) in *Herdmania*. According to Berrill the digestive enzymes are poured into the gut only by the liver; although it is doubted that the liver of Tunicata is homologous with that of the vertebrata. In the liver the secretory cells are restricted to the distal parts of liver tubules while proximal regions contain mostly absorptive cells. The same is true of *Herdmania*. In these the pyloric gland serves as an accessory organ of digestion, and is pancreatic in nature. In these animals carbohydrate is stored as starch-granules in the liver and to a small extent in the oesophagus, stomach and intestine (Fig. 1.12).

Respiratory System. The branchial sac is the main respiratory organ of the Tunicata. It has rich supply of the blood vessels which exchange gases with fresh sea-water drawn in by the efficient ciliary mechanism of the branchial sac. The area of gaseous exchange is further increased by the folds of the wall towards the side. In some cases, as also in *Herdmania*, the general external surface of the test performs respiratory activities, exchange of gases taking place through it readily.

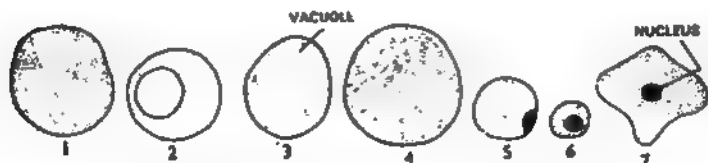


Fig. 1.15. Blood corpuscles of different types. 1-7 correspond with i-vii in the description below

Circulatory System. The circulatory system consists of a tubular heart, blood vessels and the circulating fluid, the blood. It is one of the notable features of the Tunicata that the circulation is not constant in direction but is periodically reversed that means, at one time it pumps blood in one direction and at another in the opposite direction.

The blood (Fig. 1.15), is mainly transparent, but usually contains certain pigmented corpuscles in addition to many ordinary colourless amoeboid cells or leucocytes, of which seven types have been described in *Herdmania pallida*. These include: (i) nearly spherical, large non-nucleated corpuscles containing uniformly granulated orange-coloured protoplasm; (ii) non-nucleated spherical corpuscles containing a single large vacuole; (iii) nearly spherical, non-nucleated yellowish green corpuscles containing four to five large and small vacuoles; (iv) very large, non-nucleated, highly vacuolated corpuscles containing light yellow pigment granules; (v) eosinophilous corpuscles, smaller than those of the first four types, containing uniformly granulated cytoplasm

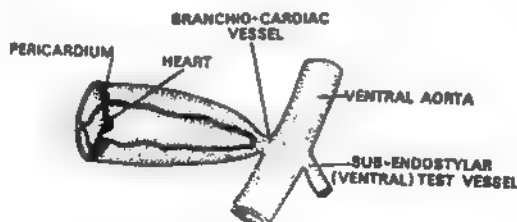


Fig. 1.16. Wall of the pericardium cut open to show the attachment of heart

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with brown pigment granules and a large eccentrically situated nucleus, (vi) very small corpuscles each with a large central nucleus and cytoplasm with uniformly distributed light brown pigment; (vii) colourless nucleated amoeboid leucocytes, capable of amoeboid movement

The heart is tubular and lies enclosed within the pericardium (Fig. 1.16), a closed transparent, non-contractile tube lying ventrally to the right gonad. It is a part of the original coelom extending obliquely from about the middle of the endostyle to about the level of the lower border of the right lobe of the liver. At both the ends the pericardial tube is closed and is filled with a colourless fluid with corpuscles. The heart is also a cylindrical contractile tube attached to the wall of the pericardium by means of a thin mesentery-like flap. The thin and convoluted wall of the pericardium (Fig. 1.17) consists of a single layer of epithelial cells surrounded by a thin layer of striated¹ muscle fibres. The two ends of the heart are open and communicate with the large blood sinuses leading to the branchial sac, to the viscera and to the body wall and test. The heart has no valves dividing its lumen.

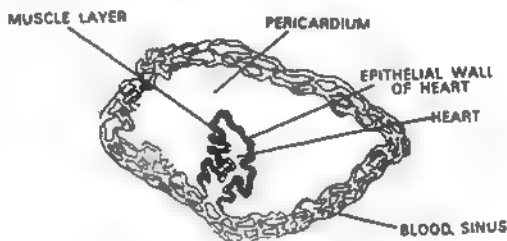


Fig. 1.17 Transverse section of the pericardium and the heart (after S. M. Das).

The blood-vessels are many and well developed. There are three main systems of blood channels, the branchio-cardiac, the cardio-visceral and the branchio-visceral, in the body of an ascidian. From the ventral end of the heart originates the branchio-cardiac vessel which soon gives off a branch to the test and then runs forwards along the ventral edge of branchial sac as the branchial aorta (called ventral aorta by S. M. Das in *Herdmania*). It runs external to the endostyle and communicates laterally with the ventral ends of all the transverse vessels of the branchial sac. At the other end of the heart arises the cardio-visceral vessel which gives off a branch to the test and then breaks up into a number of sinuses which supply the alimentary canal and other viscera. These visceral blood vessels communicate with a third great sinus, the branchio-visceral vessel, which runs forward along the dorsal edge of the branchial sac as the dorsal aorta. It is external to the dorsal lamina and communicates with the dorsal ends of all the transverse vessels of the branchial sac. Besides these main sets of blood vessels there are numerous lacunae in all parts of the body which communicate with one or the other of the main blood channel.

The course of circulation of blood is peculiar as mentioned above. For a time the blood is pumped into the branchial sac where it becomes oxygenated. Then the direction of the flow changes. The oxygenated blood returns to the heart and is pumped back into the viscera and mantle where food products and metabolic wastes are added. The flow reverses again carrying deoxygenated blood and absorbed food to the branchial sac and elsewhere. Thus it is evident that the heart acts as a respiratory pump at one time and systemic pump at another. This can be compared to the pulmonary and systemic circulations of mammals. Such a rhythmically reversed circulation presents, physiologically speaking, an example of double circulation peculiar to the Tunicata in the entire animal kingdom.

¹ This is the only instance of the occurrence of striated muscle fibres in the body of the ascidian.

Why the wave of contraction of the heart is reversed? It has been suggested that the cause of this remarkable reversal is very simple. The heart is on the ventral vessel which is wider than corresponding dorsal vessel. The heart pumps the blood into either the blood spaces of the branchial sac or those of the viscera in greater volume than can possibly get out through the smaller branchio-visceral vessel in the same time. Consequently the lacunae in question soon become engorged, and by back pressure cause the stoppage and then reversal of the beat. The absence of any valves in the heart to regulate the direction of flow obviously facilitates this alternation of the current. In *H. pallida* a pear-shaped body has been described as moving to and from in a direction opposite to that of the wave of contraction of the heart. When the flow of the blood is to right side this body moves to the left and when the flow is to left it moves to the right. Probably it functions as a mobile valve preventing flow to the left when the blood is being pumped to the right and vice versa.

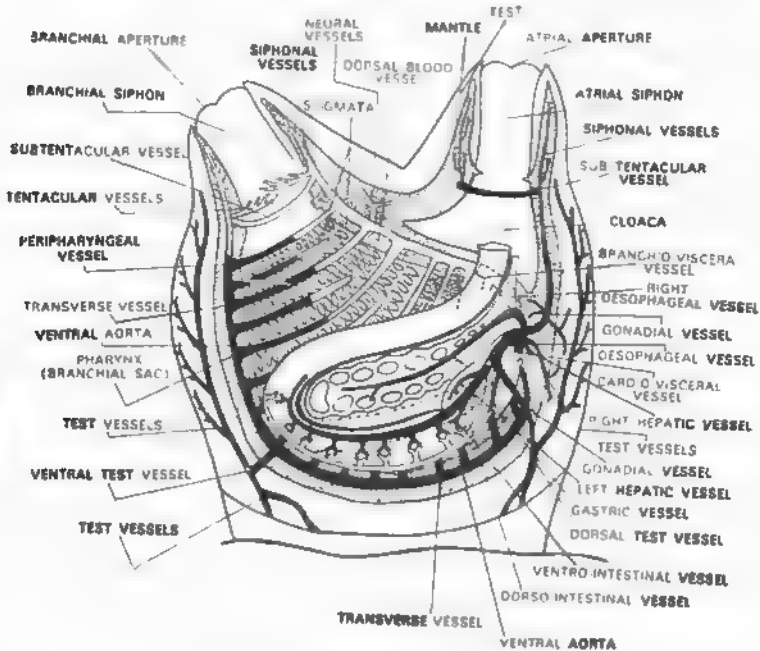


Fig. 1.18. Blood-vessels of *Herdmania pallida* (after S. M. Das).

Nervous System. The nervous system of the adult tunicate is very poorly developed for a chordate. There is a single, elongated solid ganglion, the **brain**, in the median dorsal line between the branchial and atrial siphons, the space representing all that is left of the dorsal body wall. It is made up of rounded nerve cells surrounding interlacing nerve fibres in the centre. Nerves arise from both the ends of the ganglion and divide up to supply the sphincter muscles of the oral and atrial siphons, the velum and other parts of the neighbourhood. In *Herdmania* five nerves have been described. Of these three are anterior and tend to encircle the branchial siphon and two are posterior running around the atrial siphon.

There are no well-defined sense organs in the adult tunicate, but sensory cells of various kinds occur in several organs such as siphons, velum and other movable parts: (i) the **pigments spots** or "ocelli" formed of modified ectoderm cells imbedded in red and yellow pigment, occur between the branchial and atrial siphons. These probably act as ocelli in the absence of true eyes. (ii) The **tentacles** at the base of the branchial siphon are supplied with nerves and special sensory cells and are very sensitive. Probably they can test the quality of water entering in. (iii) The **epithelial cells** covering the vascular ampullae are supplied with fine nerve fibrils and are tactile in nature. Tactile receptor cells also occur toward the outer surface of the test (iv) The **dorsal tubercle** is also believed to be sensory in nature. The dorsal tubercle is horse-shoe-shaped structure in *Ascidia mentula* situated in the dorsal part of the prebranchial zone. Its structure varies in most-ascidians according to the genus and species. Its epithelium possesses special sensory cells with rich innervations, which suggests a sensory function. According to early workers it is olfactory in nature. Recent view suggests them to be either olfactory or gustatory. (v) Sensory cells have also been found in the dorsal lamina and the endostyle. Considered as organs of special sense these are all in a lowly-developed condition. The larval ascidians, on the other hand, have well-developed intra-cerebral optic and otic sense organs. Some pelagic tunicates possess otocysts and pigment spots in connection with the brain.

Excretory System. The excretory function has been assigned to various organs of doubtful functions. The refringent organs (Botryllidae), the pyloric gland (Cynthiidae), the renal vesicles (Ascididae), the parietal vesicles (Cynthiidae) and the neural gland of all ascidians are structures believed to be excretory organs. The **neural gland** is an oval or elliptical mass of light brown cells lying imbedded in the mantle on the ventral surface of the nerve ganglion in most ascidians but dorsally in *Herdmania pallida*. The gland consists of a large number of branching tubules opening into a long non-ciliated central canal running along the whole length of the gland. This canal leads into a duct that runs anteriorly and opens by a ciliated funnel-shaped opening in the middle of the basal part of the dorsal tubercle. A single layer of small, non-ciliated rounded cells containing large nuclei forms the lining of the lumen of the gland as well as its ducts. The rest of the gland consists of a large number of small dark granulated cells. These cells are discharged into the lumen of the gland whence they pass out into the branchial cavity. The dark granules are probably excretory products.

Julin considered the neural gland to be the homologue of hypophysis cerebri of the vertebrate brain. Metcalf showed that the neural gland is partly cerebral and partly stomodaecal, as in invertebrates, and believed that the opening of the gland in the

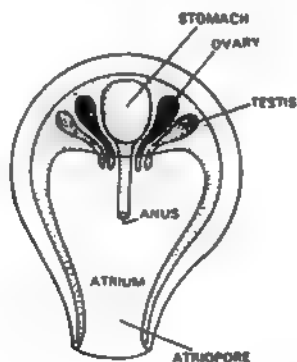


Fig. 1.19. Diagrammatic section of an ascidian to show the position of gonads

pharynx is a modified neuropore. Its function still remains doubtful. There are three possibilities: (i) It may merely form the viscid secretion which is carried along the peripharyngeal bands and down the dorsal lamina. (ii) It may be just a lymph gland. (iii) It is probably excretory in nature. In *Herdmania pallida* it is the only excretory organ.

In *Ascidia mentula* a mass of large clear walled vesicles, the renal vesicles, occupy the rectal loop, and may sometimes extend over the adjacent walls of the intestine. The renal organ is without a duct. The vesicles represent the vestiges of the coelom and each is formed of cells which eliminate nitrogenous wastes from the blood circulating in the neighbouring blood-lacunae. The waste is deposited in the lumen in the form of concentrically laminated concretions of a yellowish or brownish colour, sometimes covered with chalky deposits. These deposits carry uric acid. The nitrogenous waste is stored here instead of being excreted. The renal organ may differ in position and structure in other tunicates.

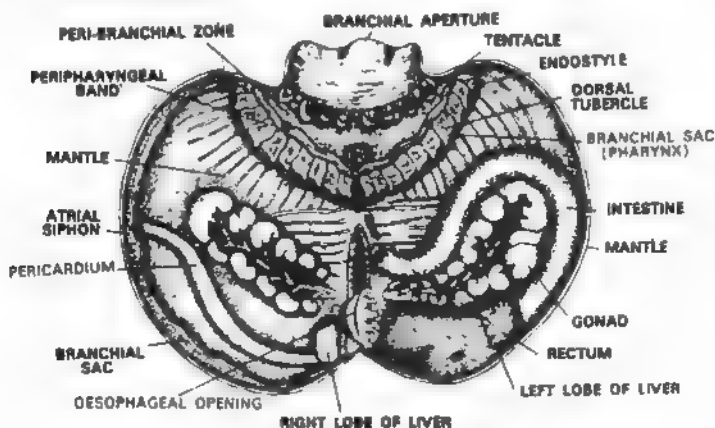


Fig. 1.20. Dissection of *Herdmania* to show the gonads and internal organs (after S.M. Das).

Reproductive Organs. The ascidians are generally hermaphrodite. In *Ascidia mentula* the gonads lie with the alimentary canal on the left side of the body. In some ascidians (certain Molgulidae and Cynthiidae) reproductive organs are present on both sides of the body and the same is true of *Herdmania* in which both are embedded in the mantle and bulge out into the peribranchial cavity (Fig. 1.20). The left gonad lies in the loop of the intestine and the right one occupies a space dorsal to the heart. In *polycarpa* there are many complete sets of both male and female systems attached to the inner surface of the mantle on both sides of the body and projecting into the peribranchial cavity.

The ovary (Fig. 1.21) is a much-branched gland and contains a cavity derived from embryonic coelom. The ova are budded off from its walls and when mature fall into the cavity. In continuation with the cavity of the ovary arises the oviduct and runs forward alongside the rectum opening into the peribranchial cavity near the anus. The testis (Fig. 1.21) is composed of a great number of delicate branched tubules which ramify over the ovary and the adjacent parts of the intestinal walls. These tubules terminate in oval swellings and near the commencement of the rectum the large tubules unite to form the vas deferens, a tube of considerable size, running along the rectum and opening into the peribranchial cavity near the anus. It is a cavity also derived from embryonic mesodermal cavity, i.e. coelom. The cells lining the wall produce the spermatozoa.

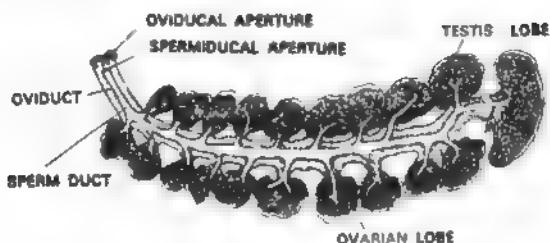


Fig. 1.21. Gonad of the left side seen from its inner face (after S. M. Das).

In *Herdmania* separate ovaries and testes have not been described. Each lobe of a gonad is hermaphrodite. It consists of two zones an outer or peripheral containing spermatid caeca and an inner containing ova in all stages of development. These two zones can be distinguished by appearance and coloration alone. The testicular region of an adult is large, papillated in appearance and brick red in colour. The ovarian region is small light red or pink in colour and because of the presence of ova it shows a large number of rounded areas. From all ovarian lobes arise short ovarian ductules and pass into a wide oviduct, which is also pink in colour and is usually packed with mature eggs. The female pore is guarded by four thick lips. The vas deferens is narrow and receives a sperm-ductule from each of the lobe of the gonads. It opens on a small thickwalled papilla, a little behind the oviducal aperture.

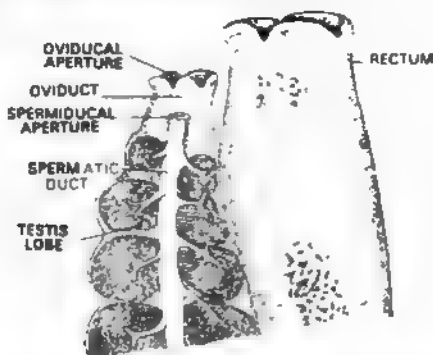


Fig. 1.22. Rectal opening with the opening of the gonoducts.

Sex-cells. Each sperm is a microscopic structure having an acrosome (or beak), a head, a neck (or middle-piece) and a long straight tail. Different types of sperms have been described. An ovum is comparatively large structure having an outer chorion to which are attached the vacuolated outer follicle cells, an inner chorion lying beneath the outer, and the vitelline membrane forming the wall of the ovum. Between the two chorionic layers lies the interchorionic fluid whereas the perivitelline fluid surrounds the vitelline membrane. A dense mass of yellowish yolk-substance is distributed in cytoplasm and the nucleus is relatively large, with a large nucleolus, and is excentric in position.

Embryology. The eggs of Tunicata are for the most part of small size nearly colourless and transparent with little or no food-yolk. Self impregnation is usually rendered impossible by ova and spermatozoa becoming mature at different times. The

ascidian egg is typically small and pelagic, but within itself it has sufficient substance for the production of cells numerous enough to establish a miniature ascidian. For instance, the egg of *Ascidia* and *Ciona* is able to subdivide to form 2,500 to 3,000 cells before minimal cell sizes are reached and cleavage comes to an end. The egg of the ascidian, therefore, falls into the category of those that contain within themselves all the material necessary for the development of the permanent organisation in miniature, and all ascidian eggs develop to this stage without gaining any additional substance on the way. The capacity to gain and digest food from external sources comes only after the development of the egg has completed when cells are no longer dividing and histological maturity has been attained. The eggs are released in the surrounding water where they are fertilized.

Cleavage. Segmentation is complete (Fig. 1.23) and results in the formation of a spherical blastula with a small segmentation cavity. At the eight-cell stage four cells are smaller, the endoderm (hypoblast), and four cells are larger, the ectoderm. In the 16-cells stage the large ectoderm cells multiply rather rapidly and become smaller and lie on one side and the endoderm cells on the other. The ectoderm cells now become smaller in size and the endoderm larger. Invagination of the larger cells then takes place forming a gastrula enclosing an archenteron (Fig. 1.23). The smaller cells at the same time grow over the endoderm cells. Gastrulation is a process of invagination accompanied by epiboly or overgrowth. The wide blastopore then gradually becomes constricted - the closure taking place from before backwards. The embryo now elongates in the direction of the future long axis. The dorsal surface becomes recognisable by being flatter while the ventral surface remains convex. Around the blastopore the ectoderm cells form a medullary plate along which a groove runs forwards bounded at the sides by medullary folds, which meet behind the blastopore. Underneath the medullary groove the endoderm cells form the dorsal wall of the archenteron in the median line form a band extending forwards. This band separates off from the hypoblast and gives rise to the notochord.

The more lateral cells of the wall of the archenteron separate off as lateral plates and become mesoblast which show no trace of metameric segmentation. The remainder of the archenteron becomes the branchial sac and by further growth buds off the alimentary canal.

The neural canal, formed by the growing up and arching inwards of the medullary folds now differentiates into a tubular dorsal nervous system. The anterior end dilates to form the thin-walled cerebral vesicle containing the later intra-cerebral, dorsal pigmented eye and the ventral otolith of the larva. A ciliated diverticulum of the anterior end of the enteric cavity enters into close relations with the front of the cerebral vesicles. This evidently is the rudiment of the neural duct or hypophysical canal. The embryo now becomes pear-shaped, the narrow part being the rudiment of the future tail. The caudal region increases in length rapidly and the anterior trunk region becomes oval (Fig. 1.23 G).

The embryo hatches about 2 or 3 days after fertilisation as a larva or *ascidian tadpole* (Fig. 1.23 H) which leads a free swimming existence for a short time, and is a transient non-feeding stage. Tadpole larva is uniformly small (about) 1.0 mm. long) and has an ovoid trunk and slender tapering tail. The trunk contains the rudiments of future ascidian structure (Fig. 1.24, 1.25). At its anterior end the trunk bears three adhesive papillae. A sensory vesicle consisting of a sac, the floor of which supports a unicellular otolith, and bearing a multicellular ocellus on the dorso-posterior wall (Fig. 1.23 H) is a characteristic. The ocellus consists of three lens cells associated with a pigmented cup formed by about a dozen pigmented sensory retinal cells (Fig. 1.24). The tail consists of a simple epidermal sheath supporting a cuticular fin and encloses a dorsal hollow neural tube extending from the sensory vesicle to the tip of the tail, a notochord below the nerve cord and made up of 40-42 vacuolated cells in a single column, and a band of striated muscle tissue on either side of the notochord (Fig. 1.24). This stage is the highest in its chordate organisation, when the larva swims actually through the sea, by vibrating its long tail. It is unquestionably a chordate, more advanced than *Amphioxus* in some respects. The notable chordate characters of the larva include:

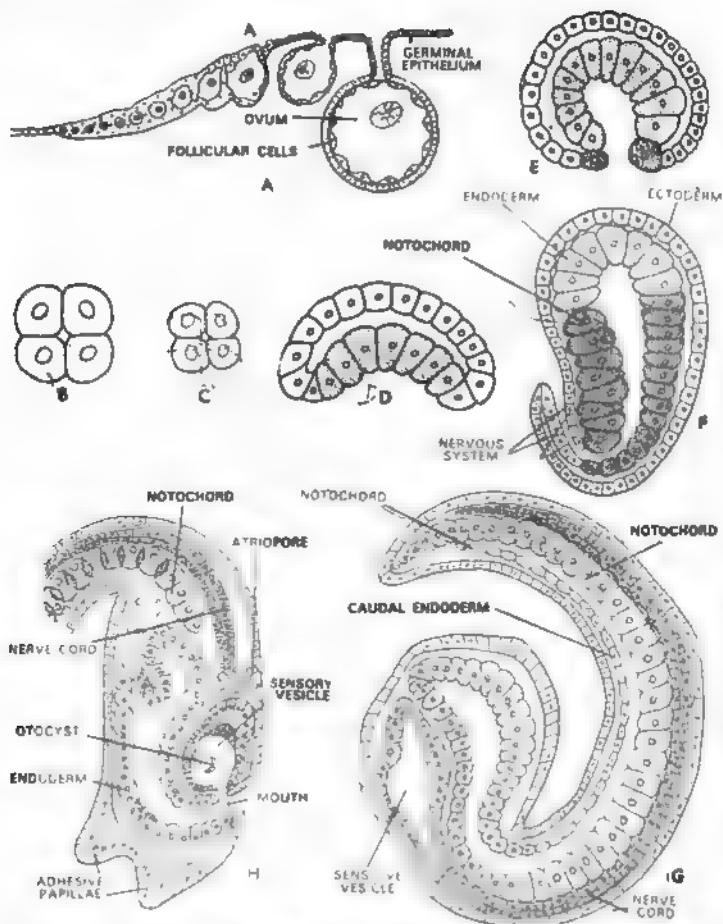


Fig. 1.23. Stages of the development of the egg and embryo. A, formation of egg. B, and C, cleavage begins. D, gastrulation begins. E, gastrula, and F, advanced embryo. Development of the tadpole larva of ascidian, G, earlier stage. H, later stage.

(i) Dorsal tubular nervous system which is enlarged at the anterior end forming "a good little brain" (sensory vesicle).

(ii) The sensory vesicle anteriorly opens into the pharynx near the mouth at a place called neuropore, probably homologous with that of *Amphioxus*.

(iii) The brain has a single median eye derived from the internal wall of the hollow vesicle and possesses retina, pigment layer, a lens and cornea—it is more specialised than that of *Amphioxus*.

(iv) Presence of an organ of equilibrium otocyst, on the ventral floor of the sensory vesicle.

(v) Notochord is present unmistakably, but is restricted only to the tail region, it

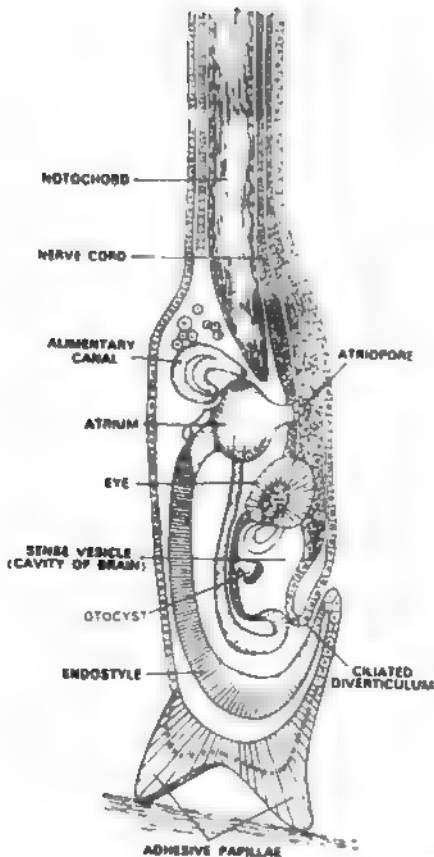


Fig. 1.24. Section of the anterior end of the tailed larva of an ascidian.

does not extend into the pharyngeal region, although it actually extends into the trunk region of the body

- (vi) Well-developed pharynx with endostyle and two pairs of stigmata is present.
- (vii) The atrium and the postpharyngeal portions of the digestive tract are in the early stages of development.
- (viii) Tail presents well-developed dorsal fin-folds.
- (ix) The anterior end bears special papillae for attachment
- (x) The heart and pericardium develop as diverticulum from the stomach.

Metamorphosis. The free-swimming life of the larva is very short as it is without any arrangement for feeding. It swims for a few hours or so or even almost for a day, then becomes sluggish, sinks to the bottom and attaches itself by the anterior adhesive papillae or "chin warts" as they have been called by some authors. For some time it stands erect, head down and then enters into a phase of metamorphic changes, in which some already differentiated tissues are lost and some undergo differential

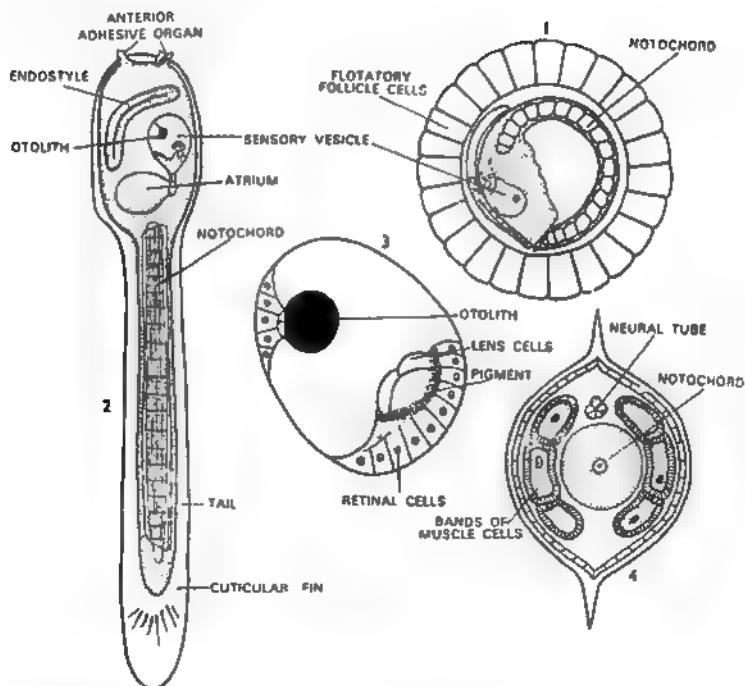


Fig. 1.25. Ascidian tadpole. 1, tadpole ready to hatch showing sensory vesicle about 40 notochord cells. 2, tadpole with anterior adhesive organs, tail with muscle band, notochord and cuticular fin; 3, sensory vesicle showing unicellular otolith and ocellus with three lens cells, pigment and about a dozen retinal cells, 4, cross-section of tail to show central notochord, bands of muscle cells and dorsal neural tube

growth Such a metamorphosis is called **retrograde** or **retrogressive metamorphosis** (Fig. 1.26)

Very rapid increase of test takes place. The entire tail with its notochord is partly withdrawn and absorbed by phagocytosis (Fig 1.26 B) and partly it is cast off in shreds. The posterior part of the nerve tube disappears with the tail, and the anterior end with its promising little brain degenerates. The remaining part is reduced to form a small ganglion of the adult, underneath which the neural gland is formed. With the degeneration of the locomotory, nervous and sensory organs there is a progressive growth of the digestive and reproductive organs. The branchial sac enlarges, gill-slits multiply in number and the atrium is extended. The stomach and intestine develop as an out-growth from the back of the branchial sac at the side. The region of the body between the point of fixation and the mouth, which is morphologically ventral, increases rapidly in extent and the true dorsal region stops growing and degenerates. The result is that the body of the growing adult rotates through 180° and the branchial siphon is carried to the end opposite to that of attachment. Thus a degenerate, sedentary fixed adult is formed with little or no trace of chordate characteristics so marked in the larval stages. This degenerate adult has been described by some authors as "an animate food-sieve with necessary accessories for digestion, circulation, excretion of wastes, and just enough brain to regulate the activities" (Newman).

The changes involved in the retrogressive metamorphosis are:—

1. Increase in the number of pharyngeal stigmata.
2. Diminution and eventually complete disappearance of the tail with the contained notochord and the caudal part of the nerve cord.
3. The disappearance of the sense organs.
4. Dwindling of the central part of the nervous system to a single ganglion.
5. Formation of the reproductive organs.

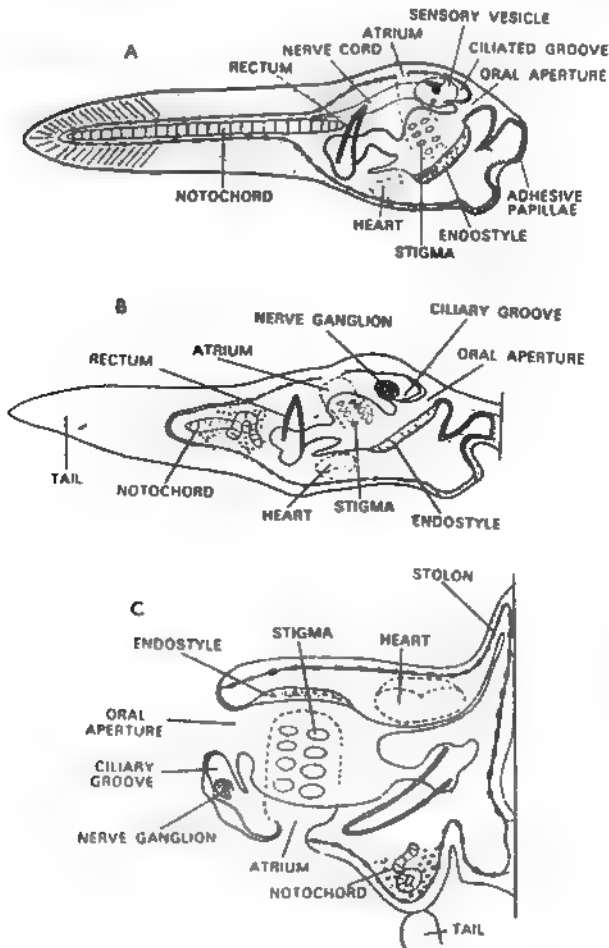


Fig. 1.26. The free-swimming tadpole metamorphoses into the sessile adult (from Parker and Haswell, after Seelinger).

TYPE DOLIOLUM

Doliolum is a free swimming pelagic relative of ascidians with transparent gelatinous test belonging to a family of the order Thaliacea that inhabit warm water. At the present time the pelagic tunicates are represented by *Doliolum*, *Salpa*, *Pyrosoma* and the *Larvacea*, which fundamentally exhibit the same basic plans of construction. In spite of their free, non-attached existence all are ciliary-feeders and create feeding currents, which cause the individuals to move forward by what is virtually jet-propulsion. All the existing pelagic types have departed much from the primitive condition, and only an intimate analysis reveals the true nature of their primitive tunicate ancestor.

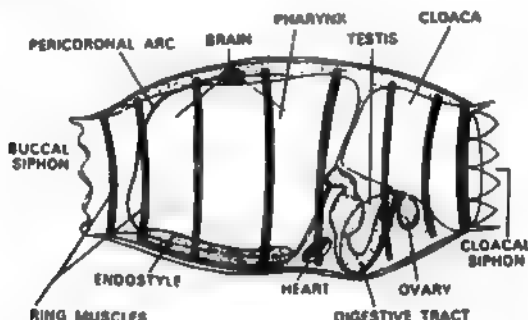


Fig. 1.27. Sexual generation of *Doliolum mulleri* from left side.

In *Doliolum* (Fig. 1.27) the muscles of the body wall are characteristically arranged in distinct bands encircling the body wholly (Cyclomyaria), while in its close ally *Salpa* the muscles encircle the body partially (Hemimyaria). The most characteristic feature of the life-cycle of *Doliolum* is that the sexually mature adult, the gonozooid, alternates with the asexually reproducing phase, the oozoid. These two phases are structurally different. Some other stages such as the phorozoides and the gasterozooides are also produced during the course of the life-cycle, they are discussed at their appropriate places. There are about a dozen known species of *Doliolum* of which *Doliolum tritorus*, *D. mulleri* and *D. rarum* are the best known species.

Structure. The body of *Doliolum* is barrel-shaped with mouth and atriopore at opposite ends, instead of being close together at the same end of the body (as in ascidians). This evidently has influenced the relation of the various internal organs. The open ends of the barrel are fringed with lobes or tentacles and represent elaborate oral (branchial) and cloacal (atrial) funnels. The body is covered by a thin, tough and transparent layer, the tunic or test, which is without characteristic test cells. It looks like thin cuticle covering the surface of the squamous ectoderm. The size of the different species of gonozooids ranges from about 3 to 12 mm. while 8 or 9 mm. is typical.

Body Wall. The body wall consists of a single-layered epidermis consisting of flat polygonal cells. It is covered by a thin layer of tunic which is without cellulose and without cell partitions. Below the internal face of the epidermis lies the mesenchyme which condenses to form the characteristic muscle bands or ring muscles of the body. There are eight ring muscles in the gonozooid and nine in the oozoid passing right round the body. Of these the most anterior one forms the branchial sphincter and the posterior one the atrial sphincter. The sphincters serve to open and close the oral and atrial apertures.

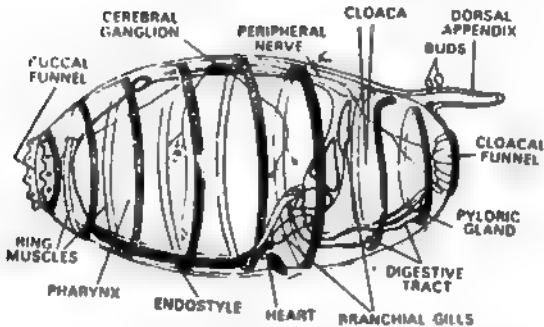


Fig. 1.21. The oozoid of *Dolioletta sacrocaeca* with a well-developed dorsal appendix.

Branchial and Atrial Sacs. The wide branchial aperture opens into a large sac, the pharynx or branchial sac occupying the anterior two-thirds of the body, the atrial or cloacal chamber occupies most of the posterior third. The lining of the atrial chamber more or less envelops the viscera (i. e. digestive loop, heart and gonads). The two chambers are separated from each other by the posterior and posterolateral wall of the branchial chamber. The branchial wall is little more than a thin membrane perforated by a dorsal and a ventral row of gill-slits. In the gonozooid each side of the branchial wall has sixty or more elongate gill-slits, which are generally regarded as primary gill-slits. In the oozoid, on the other hand, only four primary gill-slits are present on each side. A distinct endostyle is present on the ventral edge of the branchial sac, but the dorsal lamina along its dorsal edge is absent. According to some authors (Garstang and Platt, 1928) although the endostyle retains its basic structure of a long open groove (as in other ascidians), yet the edges of the groove roll up in such a way as to form a long closed tube opening only in front, so that the mucous destined to form the food trap is driven forward to be released by way of the peripharyngeal bands, which as in other tunicates, are situated on the anterior end of the branchial sac.

The arrangement of the branchial and atrial chamber is such that the water gets a free passage through the body along its long axis. The terminal anterior and posterior position of the oral and atrial funnel (siphons) is obviously related to the creation of effective water current and to the movement of the animal in water. The other factors that help the creation of the water current include the relative posterior position of the ciliated gill-slits, the effective anterior release of the mucous sheet and the system of ring muscles. The water enters through the posterior end like a jet. This is brought about by the contraction of the ring muscles and enables the animal to shoot forward (jet propulsion) which constitutes the main means of locomotion.

Digestive Tube. The individual, whether oozoid or gonozooid, is well adapted as pelagic filter feeder. The digestive tube consists of the oesophagus, stomach and intestine. The oesophagus arises from the ventral edge of the posterior end of the pharynx in the sagittal plane. The opening of the oesophagus is funnel-shaped and from its border arises a crooked retropharyngeal band of cilia. The wall of the oesophagus consists of a single layer of cells which are non-ciliated except at the retropharyngeal band which extends as far as the cardiac aperture. Ventrally the oesophagus dilates to form the stomach, which presents a triangular appearance in a transverse section. The ciliary band of the oesophagus continues on the dorsal surface of the stomach. The orifice is uniformly provided with a bush of cilia. The stomach is prolonged into intestine, which runs posteriorly, curves dorsally forming a ventral convex arch not unlike the handle of a cup and opens into the floor of the peribranchial (cloacal) chamber at the anus. The wall of the digestive tube is without musculature.

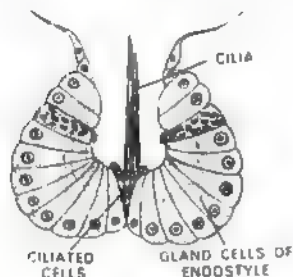


Fig. 1.29 Cross section through the endostyle of *Doliolum*

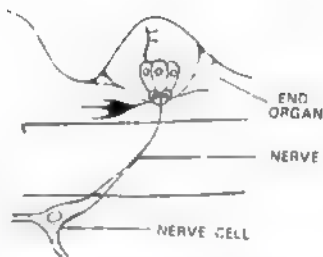


Fig. 1.30 Sensory cell of *Doliolum mulleri*

Nervous System. The nervous system consists of a cerebral ganglion and peripheral nerves arising from it. The cerebral ganglion is ellipsoid, enveloped by a fine connective tissue membrane. It is situated within the intermuscular space in the dorsal edge of the body usually between the third and fourth muscle bands. It consists of a central fibrous mass surrounded by a cortex made up of 1-3 layers of ganglion cells. From the ganglion arises an anterior median dorsal nerve which innervates the first two muscle bands and the buccal region, a posterior median nerve descending to the branchiae, and three pairs of lateral nerves, which innervate the different visceral organs. The finer ramifications of these nerves mostly end in sensory organs, most of which are tactile in nature (Fig. 1.30). The number of the sense organs on the lobes of the oral and cloacal aperture is more than that on the epidermis. They also differ in shape from each other. In the oozoid generation on each side of the body occurs a statocyst where one of the lateral nerve branches terminates. It is not present in the gonozooid. An ocellus is absent.

Neural Gland. The neural gland is situated below the cerebral ganglion. The gland is prolonged into a narrow duct, which runs forward and opens into the anterior end of the pharynx (branchial sac) by a simple aperture surrounded by the spirally twisted dorsal ends of the peripharyngeal bands. As in other Tunicates the neural gland with its duct and the cerebral ganglion are derived from the embryonic neural tube.

Heart. The heart is situated within an elongated oval vesicle, the pericardium, placed mid-ventrally between the posterior end of the endostyle and the oesophageal aperture. The pericardium is a closed transparent non-contractile tube enclosing a part of the original coelom. The heart is also an elongated tube communicating with blood vessels at both the ends. It resembles the heart of the ascidians already described. From the heart blood vessels arise as in the ascidians and maintain circulation in the body. The blood consists of clear plasma in which float ordinary colourless amoebocytes which are capable of producing long pseudopodia. The blood circulates through hollow blood sinuses as in other Tunicates.

Dorsal Appendix. The oozoids of *Doliolum* possess a dorsal appendix situated between 7th and 8th muscle bands. It is a rigid immobile structure, enlarged at base and slender at the extremity. It is covered by tunic which is more thick at one place and less at other. The appendix consists of a process of body wall into which extends the haemocoel which is delimited by ectoderm. The ectoderm consists of flat cells except on the dorsal face where the cells are cylindrical. Internally the mesenchyme encloses two hollow sinuses separated by mesenchymatous septum. Therefore two currents of blood flow through the appendix, one along with the general circulation of the body, and the other opposite to it, one out-going and other re-entering.

Stolon. On the ventral face, behind the endostyle, the oozoid gives off a small median ectodermal diverticulum covered by tunic. Some authors (e.g. Keferstein and

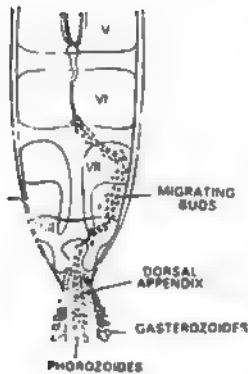


Fig. 1.31. Migration of buds in *Dolioletta gegenbaumi*.

Ehlers) attribute excretory function to it, but in reality it is a stolon for proliferation during budding.

Reproduction takes place by budding as well as by the production of eggs and sperm. Budding takes place in the individuals that develop from eggs (oozooid) while one of the individuals produced by budding develops gonads (gonozooid). The oozooid has a budding stolon but does not develop gonads, the gonozooid, on the other hand, develops gonads but lacks a budding stolon. The sexually reproducing generation (gonozooid) alternates, with the asexually reproducing generation (oozooid).

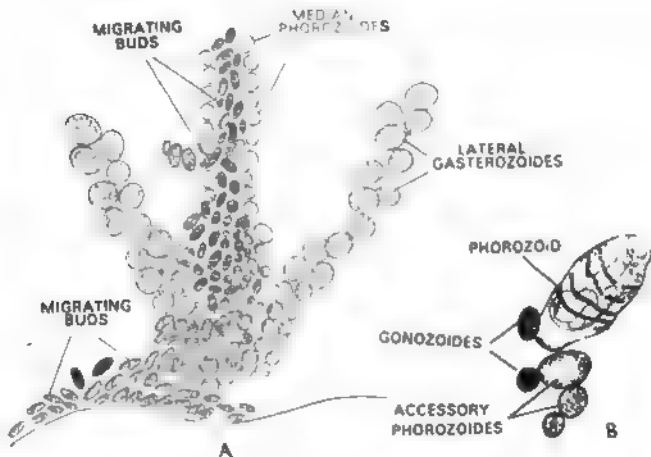


Fig. 1.32 A, disposition of buds on the dorsal appendix B, Gonozooids and phorozooids of *Dolioletta* (enlarged).

Sexual Reproduction. *Doliolum* is hermaphrodite. Both the ovary and testes lie to the left of the middle line alongside the alimentary canal and their ducts open in the atrial cavity. The ovary is pyriform or nearly spherical, while the testis is very variable in form in different species. It is short and narrow in *D. mulleri* while it is elongated, cylindrical or rectangular in *D. rarum*, *D. nationalis*, *D. intermedium* etc. In *D. denticulatum* the elongated testis extends anteriorly upto the region of the second muscle band.

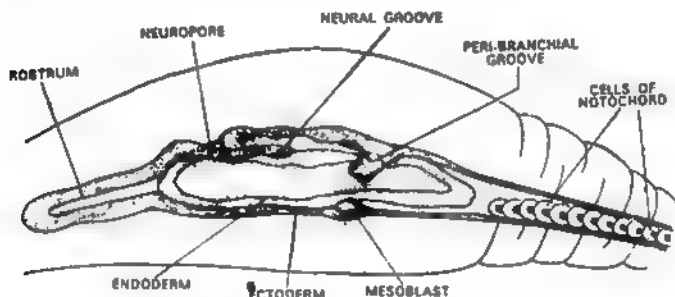


Fig. 1.33. Larva of *Doliolum denticulatum*.

Development. The eggs are very small and transparent and are shed at the time of fertilization. The cleavage is total (holoblastic) and rapid with the result that a gastrula is formed by invagination within five hours of fertilization. Soon the gastrula elongates and takes the form of a cigar (Fig. 1.35). At this stage it consists of an anterior rostral extension, a trunk region (the future individual), a large median vesicular region and a posterior tail. A large perivitelline space enclosed within the original vitelline membrane surrounds the tailed embryo. The large median vesicular region of the larva and the perivitelline envelope act as float during development. The rostral outgrowth is temporary (short-lived) and becomes the stalk. Such a rostral outgrowth appears during the development of many other ascidians (*Ciona*, *Clavelina*). So after gastrulation the tail is seen to contain about forty chordal cells. Along each side of the notochord about forty fibrillated muscle cells form a band. It is interesting to note that the structure of the notochord and number of its cells and those constituting the muscle band is just the same as found in other ascidian tadpoles. The tail has no connection with the anterior region where the neural tissue

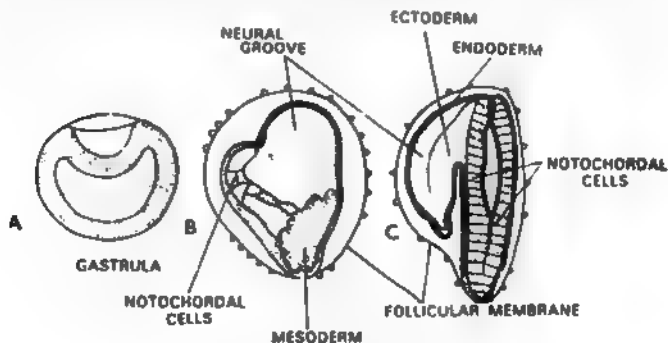


Fig. 1.34. Three stages in the development of *Doliolum mulleri*.

develops and possesses no sense organs. Further the tail is not functional. It is retained within the perivitelline membrane. It is, therefore, concluded that it is a residual (rather than primitive) organ indicating a past relationship with ascidians. Thus, it is apparent that cleavage, gastrulation and tail formation takes place as in other ascidians but larval sense organs do not develop and the larva does not settle down to attach to the substratum. Metamorphosis is re-represented only by absorption of the tail. The region which lies between the transient tail and the transient stalk is the main body of the tunicate. Soon after metamorphosis, therefore, the oozoid is formed which is characterised by nine muscle bands (not eight), fewer gill-slits confined to the posterior end of the branchial sac, and statocyst on the left side of the body, a ventrally placed stolon (rosette organ) from which primary buds arise by constrictions and a dorsal appendix (cadophore) near the posterior end of the body.

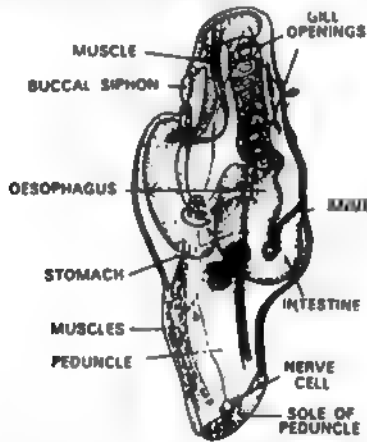
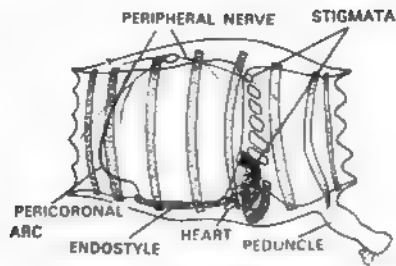


Fig. 1.35. Development of gasterozoid of *Dolioletta dentilatum*.

Budding. Bud formation takes place by successive constrictions from the distal end of the bud stolon. The buds, or probuds migrate along the surface of the parent and wander out in three lines along the dorsal spur giving rise by subdivision to the definitive buds. The migration of the buds is made possible by certain amoeboid test cells which become attached to them. Being polymorphic the buds develop into three types of individuals of which two types do not develop reproductive organs and only one becomes sexually mature forming what is known as the gonozooid. Of the two types with undeveloped reproductive organs some lateral buds become merely nutritive individuals the trophozooids permanently attached to the parent. Their development is arrested, the musculature is slightly developed and the body is elongated dorsoventrally with a large funnel-like branchial aperture. They not only aid in respiration but provide food for the parent "nurse" as well as for the growing buds of the median row.

Phorozoids. Some buds arising from the median row also fail to develop reproductive organs and form what are described as the foster forms or phorozoids. Unlike trophozooids the phorozoids have *dolioletta*-like appearance, possess eight ring muscles and a ventral outgrowth (not stolon), a remnant of the stalk by which the body was formerly attached to the cadophore of the oozoid. These cask-shaped bodies are released and they carry very young buds destined to grow into gonozooids on their ventral outgrowth. They have been called foster forms because they carry these young gonozooids, which are released when they become fully mature. The gonozooid

Fig. 1.36. Phorozooid of *Dolioletta mulleri*.

resembles the phorozooid in having cask-shaped body, eight ring muscles, but differ from it in the absence of a ventral process and in having fully developed reproductive organs.

Colonial Forms. There are two types of ascidians, **simple** and **compound**. The simple ascidians also reproduce by budding and produce complete individuals, each with a separate test. They are only mechanically connected with the parent. The compound ascidians are also produced by budding but the new individuals are buried in a common test in which occur open canals connecting the atrial cavities of groups of individuals. In some sessile tunicates the common test grows as an encrusting mass over the surface of rocks, shells or sea-weeds. The members of the colony may be arranged in groups as in *Botryllus* in which groups are so arranged as to form rosettes or stars. The mouths of the individuals are separate being at the tips of the rays of the stars whereas the common atriopore (cloacal pore) for the exit of water is at the centre of the stars.

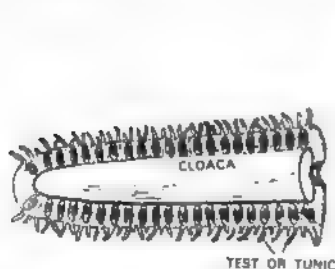
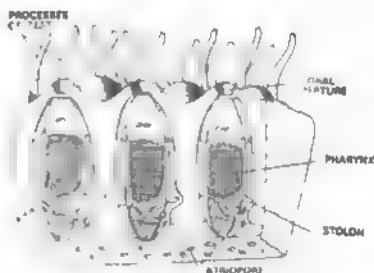
Fig. 1.37. A longitudinal section of the colony of *Pyrosoma*.

Fig. 1.38. A part of the section of colony magnified

Pyrosoma presents an interesting example of pelagic colonial form. It occurs in warm seas and comprises a number of individuals to form a barrel-shaped colony, closed at one end and open at the other. The oral funnels of all individuals (ascidiozooids) open on the outside and the cloacal funnels all open into the hollow of the cylinder with a terminal outer, fitted with a velum or diaphragm acting as a regulator of water flow. The velum also acts as an organ of locomotion, which depends on the flow of water through it. All of the ascidiozooids in the compound "individual" are oriented in the same way, with anterior end outward, posterior end inward, dorsal side toward the open end and ventral side toward the closed end of the cylinder. The outstanding characteristic of the creatures is the powerful light which they emit. This is produced by symbiotic bacteria living in special cells in various parts of the body. This light is so powerful that when large number of colonies of *Pyrosoma* occur, the whole

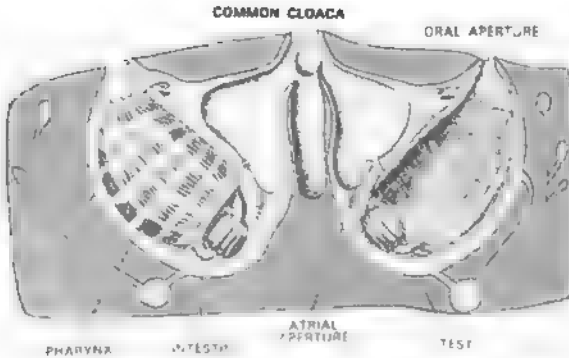


Fig. 1.39. Sectional view of a portion of colonial ascidian *Diplosoma*.

sea is illuminated so as to allow reading a book. The bacteria infect eggs and pass from generation to generation.

Phylogeny. A typical tunicate is one of the most inanimate being among chordates rivalling only a sponge in inertness. For this reason they were believed to be related to either Alcyonaria or sponges for a long time. Aristotle was the first to describe a simple ascidian under the name of *Tethyum* whereas a compound ascidian, *Botryllus* was described by Schlosser and Ellis in 1756, but, for a time their affinities remained obscure. In 1816 Lamarck, chiefly on the basis of the anatomical discoveries of Savigny (on compound ascidians in 1816) and Cuvier (on simple ascidians in 1815) instituted the class Tunicata, but placed it between the Radiata and Vermes.

It was Kowalevsky's (1866) work on the development of a simple ascidian that placed the tunicates on the right place. The tailed larva of ascidian was discovered previously, but without any clear understanding with regard to its position. Kowalevsky showed the striking similarity in structure and in development between the larval ascidian and the vertebrate embryo. He showed that the relations between the nervous system, the notochord, and the alimentary canal are practically the same in the two forms, and have been brought about by a very similar course of embryonic development. This discovery clearly indicates that the Tunicata are closely allied to *Amphioxus* and the vertebrata and the tailed larva represents the primitive or ancestral form from which the adult ascidian has been evolved by degeneration (retrogression). The following are the common chordate features of the ascidian tadpole:

(i) The central nervous system is dorsal and tubular and is enlarged at the anterior end, which opens anteriorly into the pharynx near the mouth at the neuropore (homologous with that of *Amphioxus*).

(ii) Single median eye in the brain—an eye far more specialized than that of *Amphioxus*.

(iii) An otocyst, doubtless an organ of equilibrium, is present.

(iv) Unmistakable notochord is present.

(v) The pharynx is well defined with endostyle and two pairs of stigmata.

(vi) The atrium and the post-pharyngeal digestive tract are developing.

(vii) Tail has dorsal and ventral fins.

Most of these characters are also shared by the larval *amphioxus*. Not only the larva but the adults also possess characters that establish the relationship between the tunicates and the Cephalochordata. In the adult tunicate and *Amphioxus* there exists a similar food concentrating mechanism, including velum, endostyle and its accessories and the whole atrium complex. Evidently these characters show a close homology and furnish convincing evidences of common ancestry.

During recent years most zoologists have become convinced that the tunicates are primitive and ancestral to the chordates as a whole. Accordingly the ascidian tadpole

larva is regarded a relic of a past free-swimming chordate ancestor of ascidians and the adult ascidian is regarded as secondarily sessile and degenerate only "to the extent that they have become adapted to a fixed habit of life" (Willey 1894). That means that they are not altogether degenerate forms produced by the degeneration of a complex chordate, but simple primitive forms that have lost certain parts, that were not needed as they took to fixed habit of life.

The organization of the free-swimming ancestor is generally assumed more or less like that of an *Amphioxus* or an ammocoetes, sharing an open endostyle and ciliated gill-slits with the former, and cerebral sense organs and absence of an atrium with the latter, together with the neuromuscular metamerism of both. The tailed larva of ascidian is supposed to represent such an ancestor, which having fixed itself to a rock, was eventually superseded as an adult by the modern sessile creature.

There are three objections to this hypothesis that have to be explained. These include (1) the absence of coelomic and neuromuscular metamerism, (2) the development of lateral atria before the gill-slits, and (3) the independence of larval and adult nervous systems. Garstang (1928) has explained these objections and according to him these are "possibly small matters compared with the possession by tunicate larvae of the typical vertebrate combination of notochord, gill-slits and neural canal."

It is now widely accepted that the chordates as a whole have arisen from such a free-swimming organism as the ascidian tadpole. There are evidences that the ascidian tadpoles have given rise, through neoteny, to permanently free-swimming forms (thalaceans and appendicularians). Some of these forms were attracted by "the rich detritus descending from the river systems and entered the estuaries and river mouths to the extent that their locomotory power enabled them, through elaboration of their sensory and locomotor equipment, and above all, through increase in size and by acquisition of a segmented muscle system, they finally ascended the rivers themselves. Segmentation of the body was called forth by the need to maintain or improve position in the face of down flowing fresh water current" (Berrill). *Amphioxus* is a relic of this intermediate phase, but, in this case, it seems, that *Amphioxus*, rediscovered certain advantages of marine life, probably from necessity became readapted to feeding in the same general territory as the ancestral ascidians.

The problem of the origin of the ascidian tadpole seems to be answered by Garstang's auricularia theory first propounded in 1894. This theory suggests how an ascidian tadpole has arisen from the auricularia larva, which assumes the ancestral position. Instead of adding new and powerful ciliary mechanisms for prolonging the pelagic phase, "the larval body elongated, became increasingly muscular, with an increasing tendency towards a segmented arrangement, in consequence of resorting to lateral undulations as a means of locomotion. This had the effect of bringing the lateral halves of the circumoral bands and its underlying nerve tract, into closer parallelism on either side of the mid-dorsal line." Eventually the ciliated bands rolled up with their underlying sheets of nerve plexus to form the neural tube. The adoral ciliated band might then well be the endostyle (Fig. 1 24). This theory of Garstang is "necessarily speculative", but it has certain strong marks of inherent probability.

Thus it can be reasonably concluded that (i) the tailed ascidian larva is the relic of the free-swimming chordate ancestor, (ii) which attached to the substratum, took to sessile life and became the adult sessile tunicate, necessarily a simple rather than 'degenerate' chordate (iii) Some tailed larvae became neotenuous, wandered into estuaries and rivers ultimately evolving into amphioxus-like chordates. (iv) Some of these rediscovered the advantages of marine life and out of necessity became readapted to it thus evolving the familiar chordate, *Amphioxus*.

CLASSIFICATION

Subphylum II. Tunicata (Urochordata). Remarkable ciliary-feeding marine animals -the sea-squirts and their allies. Except members of one group the most are sedentary. The chordate characters are lost in the adult. But their free-swimming larvae possess important chordate characters. The notochord is found in larval stages only restricted to the tail (hence Urochordata). A well-developed endostyle is present.

At metamorphosis the larvae settle on the sea-floor to which they adhere by means of glandular papillae on the head. Rapid growth in size takes place and the animal undergoes **retrogressive metamorphosis** with the result that (i) the larval nervous system is lost; (ii) the body becomes surrounded by a gelatinous or horny coat, the tunic or test; (iii) the number of stigmata increases and the pharynx becomes enlarged, the stigmata open into an ectoderm lined cavity the atrium, and (iv) that tail is cast off and with the tail the notochord is also lost.

There are about 2,000 species of sessile tunicates and about 100 species of pelagic forms. The subphylum is divided into 3 classes.

Class 1: Larvacea (Appendicularia). Free-swimming pelagic forms retaining larval characters in the adult stage. Two gill-slits only. Atrium is absent. The test is thin and periodically cast off (not permanent). *Oikopleura* is a common example of this group. The larvacea retain the larval form throughout adult life and are neotenous. The tail along with its supporting notochord is rather loosely articulated like an appendage to the trunk (hence Appendicularia). The body is short, lodged in a 'house' made out of test, a relatively large jelly-like dwelling with a front and a back door. The 'house' building material is produced as a secretion from a special part of skin, the 'oikoplastic epithelium'. The tail is not like that of the ascidian tadpole, it is a broad structure held at an angle to the rest of the body. It is an efficient locomotor organ supported by a notochord that does not extend into the trunk. The dorsal and ventral fin-folds of the tail of the ascidian tadpole have united to form a continuous fin-fold. The tail possesses muscles and extension of the dorsal nerve cord and its movements produce a current in which the food is carried and caught by a most elaborate filter arrangement in the house. Water enters the house by a pair of posterior 'filter windows' and is passed through a system of filter pipes in the part of the house in front of the mouth. The pharynx has two gill-slits, an endostyle and peripharyngeal bands. The presence of two gill-slits suggests that this is primitive member of urochordates and that the larger number of gill-slits in tunicates and salpians is the result of secondary polyisomerism in Gregory's sense. The general organization is like that of a typical ascidian tadpole. A large hermaphrodite gland (ovary and testis) occupies a considerable part of the posterior end of the trunk. The hermaphrodite condition and the U-shaped alimentary tract affirm that in these animals the adult stage is eliminated and the larval forms have become sexually mature and behave as normal beings for the purposes of life.

Class 2: Ascidiacea. Sedentary animals usually fixed to the substratum such as the sea-squirts. Often colonial. Reproduction by sexual method. Metamorphosis complete. Many gill-slits persistent. Test well-developed and permanent. Example include *Ascidia*, *Clavelina*, *Botryllus*, *Pyrosoma*.

Class 3: Thaliacea. Large free-swimming forms with transparent gelatinous test. Muscles of the body well arranged in distinct bands, encircling the body wholly or partially. Two distinct phases in the life history, which differ from one another structurally (Polymorphism) besides one reproduces sexually and the other asexually. Examples include *Salpa*, *Doliolum*, etc.

These are free-swimming pelagic forms, sometimes solitary and sometimes colonial, living in warm water. These represent the solid, sessile sea-squirts transfigured into beautiful gracefully swimming almost transparent forms. They shoot through the water by jet propulsion, for which purpose they possess specially developed circular muscle bands, which run right round the body (Cyclomyaria) in *Doliolum* and its allies, or the rings are incomplete (Hemimymaria) as in *Salpa*. The mouth and atriopore are at opposite ends of the barrel-shaped body. The open ends of the "barrel" are fringed with lobes, or tentacles, which represent elaborated oral and cloacal funnels. The tunic is thin and transparent, like the rest of the body, and contains no cells. The pharynx or branchial sac is large, suspended from the dorsal wall of the atrium and perforated by a dorsal and a ventral row of secondary gill-slits. Endostyle and a peripheral ciliated band are present but no dorsal lamina. The oesophagus opens out of the ventral part of the pharynx, stomach is small and intestine short, the anus opening almost posteriorly. The dorsal ganglion and subneural gland are situated a little nearer the anterior than the posterior end. They are hermaphrodite although

fully free-swimming. This suggests that they are derived from a sessile ancestor.

The most remarkable thing about these forms is the alternation of generations in the life-history. In *Doliolum* for instance, the early development is much like that of a tunicate, but the tailed larva metamorphoses, without getting fixed to substratum, into a mother or nurse zooid (oozoid). The tail with its notochord is lost. This represents the asexual generation, and, by budding, it gives rise to a string of zooids, which look like amoebae as they crawl over the surface of the parent body and locate themselves on the stolon, a dorsal process of the body wall, and proceed to grow. These buds arrange themselves in rows, the oldest being at the tip of the stolon, or form a ring. Some of these individuals grow into sexual forms, whereas some act as nutritive individuals for the benefit of the community. There are three types of individuals (i) sterile, nutritive and respiratory individuals (trophozooids), permanently sessile on the parent, (ii) sterile nurse forms (phorozoids) which are eventually set free, (iii) sexual forms (gonozooids) which are nursed and carried by the phorozoids until sexually mature, when they break off. These grow for some time and then reproduce sexually forming asexual forms. In *Salpa* the sexual form produces only a single egg, which develops within the mother, nourished by a special placenta-like organ whose cells actually migrate into the developing embryo. This develops into asexual form.

THE CEPHALOCHORDATA

Definition. Fish-like Acrania with a permanent notochord, gill-slits and a dorsal tubular nervous system, but nothing resembling a skull.

General Characters. The Cephalochordata are the acraniate chordates in which the notochord and nerve cord are persistent and extend along the entire body, anteriorly right up to the tip of the snout. The pharynx is large and sac-like perforated by numerous gill-slits. There is a prominent endostyle and a definitely ciliated tract answering the ciliary feeding habit. The gill slits open into the atrium. There is a definite coelom. Metamerism is well marked. Excretion takes place through definite nephridia. The embryonic development is complicated. The subphylum Cephalochordata includes two principal genera 1. *Branchiostoma* (*Amphioxus*) having paired sexual organs (gonadic pouches), and 2. *Asymmetron* with unilateral gonads. The amount of generic divergence exhibited by these animals is not great, but is of great importance. About eight species of *Amphioxus* and half-a-dozen species of *Asymmetron* are known so far.

TYPE AMPHIOXUS

Amphioxus (sharp at both ends) or the lancelet is the name of a small fish like marine animal forming the subphylum Cephalochordata of the phylum Chordata. They occur in brackish or saltwater, generally near the coast and have been referred to several genera and many species. P. S. Pallas first discovered them in 1778 and took them to be slugs and naturally gave the name *Limax lanceolatus*. It was in 1834 that O. G. Costa recognized its true position in the animal kingdom and named it *Branchiostoma* (genus), the name that has precedence over *Amphioxus*.

Amphioxus (Fig. 140) is of great theoretical interest, which depends upon a variety of circumstances. In the constitution of its digestive, vascular, respiratory (branchial), excretory, skeletal, nervous and muscular systems and in its manner of the development from the egg, it exhibits what appears to be a primordial condition of vertebrate organization, a condition which is in fact, partly recapitulated in the course of the embryonic development of craniate vertebrates. It provides many illustrations of important biological principles of comparative morphology and throws new light upon, or at least points the way to new ideas of, the primitive relations of different organic systems in respect of their function of topography. The absence of paired organs of special sense, olfactory, optic and auditory, which are characteristic of higher vertebrates, suggests that the animal is degenerate rather than primitive. This is a puzzle that surrounds *Amphioxus*. It is true however, that a definite gap separates this animal from the lowest fishes in many ways.

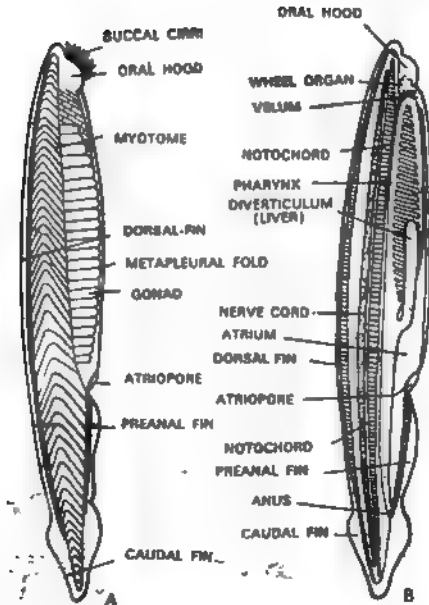


Fig. 1.40. *Amphioxus*. A, entire; B, diagrammatic sagittal section of the same showing internal structure.

Habitat. It is found in the shore water and on the sandy beaches of the temperate subtropical and tropical portions of the world. It favours a littoral habitat, and rarely, if ever, descends below the 50-fathom line. They occur on the Atlantic coast as far north as Chesapeake Bay, at certain points in the Gulf of Mexico and on the southern Pacific coast. They have also been found along the shores of the Mediterranean sea, the Indian Ocean, and along the southern coasts of China. *Branchiostoma (Doliichorhynchus) indicus*, a recently described species characterized by the great length of snout, has been dredged in the Indian Ocean.

Habit. *Amphioxus* is essentially a burrowing animal. Though none of its features is connected with burrowing life, it burrows rapidly head first, in the sand by means of vibratory action of the entire body, but comes to rest with anterior end exposed to the water. It rests with head protruding and mouth wide a gape. It is also able to swim freely in water by means of lateral strokes of the posterior-portion of the body. It leaves the burrow particularly at night and during breeding season.

External Features. *Amphioxus lanceolatus* is about two inches long (sometimes attaining a length of about 3 inches), fish-like creature, semi-transparent in appearance showing iridescent play of colour. The body is narrow, laterally compressed and pointed at both ends. The back of the body is occupied by a crest, the dorsal fin (Fig. 1.40), consisting of a hollow ridge, the cavity of which is divided into about 1.63 compartments or fin-chambers, into each of which projects a stout column-like fin-ray, made up of characteristic laminar tissue. The fin-rays may be absent in the fin-chambers near the anterior and posterior end of the body. The dorsal fin is continued round both extremities. Anteriorly it forms the expanded rostral fin and the caudal fin posteriorly. The ventral fin extends between the anus and atriopore.

For the sake of convenience the body can be divided into four regions, the **cephalic**, **atrial**, **abdominal** and **caudal**. The cephalic region includes the **rostrum** or **preoral lobe** (Fig. 1.40) and mouth. The notochord extends beyond the mouth up to the tip of the rostrum (Fig. 1.41). The mouth consists of two portions an outer **vestibule** and an inner **oral aperture**, which is surrounded by a sphincter with tentacles called the **velum** (Fig. 1.40). The vestibule of the mouth is the space bounded by the **oral hood**. The lid-like growth around the true oral aperture grows larger and downwards enclosing this space. This is fringed with tentacle-like sensory processes the **buccal cirri** (Fig. 1.40), each of which is supported by a solid skeletal axis. The oral hood with its cirri has a special nerve supply and musculature by which the cirri can be either spread out or bent inwards. They may cross each other and may completely close the entrance to the mouth. The velum is also provided with a circlet of twelve **velar tentacles** (in some species sixteen) which hang backwards into the pharynx.

The underside of the oral hood bears a complicated series of ciliated grooves and ridges collectively known to form the **wheel organ** (Fig. 1.40), because it sets up whirling currents of water. Between the ciliated lobes of the wheel organ towards the right hand side of the notochord there is a glandular groove which secretes mucous. This is called **Hatschek's pit** (Fig. 1.41).

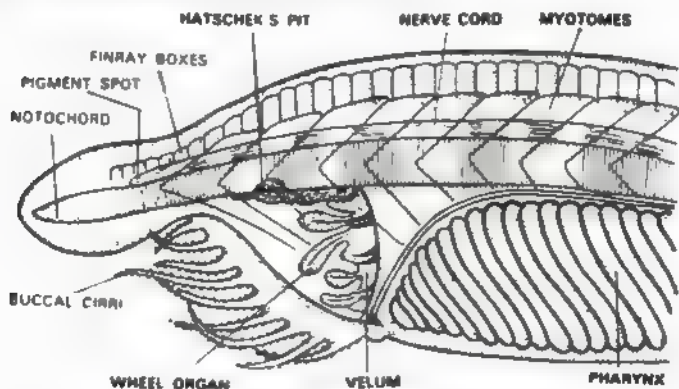


Fig. 1.41. *Amphioxus*. Parasagittal view of the anterior end.

The **atrial region** extends from the mouth over about two-thirds of the length of the body, terminating at a large median aperture, the **atriopore** (Fig. 1.41). It is an aperture for the exit of the respiratory current of water and also serves for the release of reproductive products. For this reason the atrial region has also been called the **branchio-genital region** but the external features do not indicate its reproductive nature. The ventral side of the body in the atrial region is broadened convex so that the body presents a somewhat triangular appearance, the dorsal fin forming the apex and the angles bordered by two hollow folds, the **metapleural folds**. Within each metapleural fold lies a continuous longitudinal lymph-space, the **metapleural canal**. Really speaking the oral hood is continuous posteriorly with metapleural folds on each side. In *Amphioxus*, the metapleural folds terminate symmetrically shortly behind the atripore, but in some *Asymmetron* the right metapleural passes uninterruptedly into the ventral fin.

The **abdominal region** comprises a short stretch of body between atripore and anus, the termination of the alimentary canal. It is characterized by the presence of a special **ventral fin** (preanal fin) which is composed of two portions, a lower keel-like portion lying below an upper chambered portion, each chamber containing typically a pair of gelatinous fin-rays.

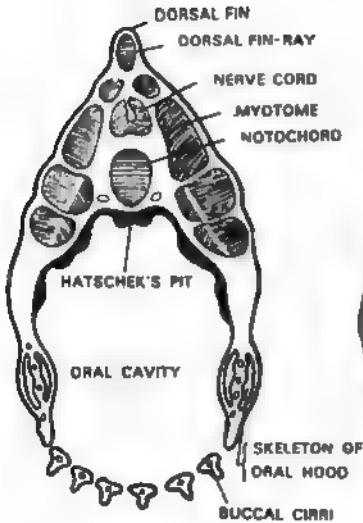


Fig. 1.42. *Amphioxus*. Vertical section through the oral cavity.

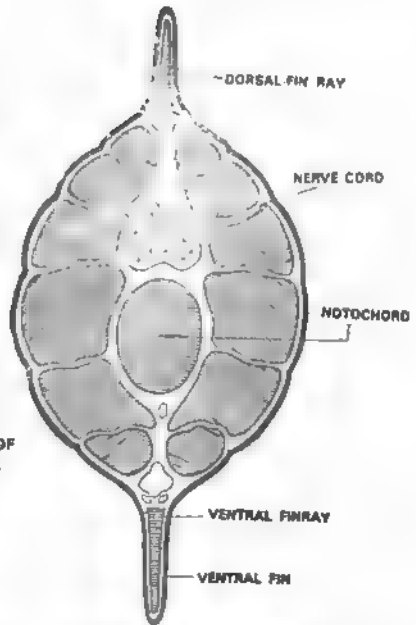


Fig. 1.43. *Amphioxus*. Vertical section through the tail region.

The caudal region includes the post-anal division of the trunk. The keel of the ventral fin is continued past the anus into the expanded caudal fin (Fig. 1.40), and so it happens that the anal opening is displaced from the middle line to the left side of the fin. In *Asymmetron* the caudal region is remarkable for the curious elongation of the notochord, which is produced far beyond the last of the myotomes.

Body Wall. The body is covered over by a thin layer of epidermis (Fig. 1.43), which differs from that of the higher chordates in being made up of a single layer of cuboidal epithelium. These cells are ciliated in the young, but in the adult the outer border becomes slightly cuticularized. Below the epidermis lies a tough connective tissue layer, distinguished into cutis and subcutis, which encloses nerve fibres and blood vessels, etc. There are no glands or chromatophores in the skin, which is more or less transparent, and the underlying musculature can be seen through it.

The musculature which forms the greater part of the body wall is made up of about sixty pairs of segmentally arranged muscle segments or blocks, the myotomes. The myotomes do not run straight down the body in dorso-ventral direction, but are V-shaped the vertices of 'V' being directed anteriorly (Fig. 1.41). Each muscle block is enclosed in a complete box of connective tissue. The anterior and posterior connective tissue walls are referred to as myocommata. The inner connective tissue walls lie just before the parietal layer of peritoneum. The olfactory pit, if present, is situated on the first muscle-somite.

These myotomes enable it to swim rapidly with characteristic serpentine undulations of the body. The movements are brought about by the alternate contraction and relaxation of the muscles on both the sides. As a result of contraction body bends, but the telescoping of the muscle segments is prevented by the notochord. The myotomes of the two sides (right and left) alternate with each other and are not opposite each

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other. This anatomical peculiarity is apparently correlated with the peculiar mode of locomotion. When the somites appear for the first time they are symmetrically placed, but they soon undergo distortion with the result that the somites of left side are carried forwards through the length of one-half segment. For instance, the twenty-seventh myotome of the left side is placed opposite to the twenty-sixth myocomma of the right side. This arrangement is responsible for the bending of the body at varying angles, as the muscles contract, resulting in a forward propagation. The body, however, is not adapted for fast movement.

Coelom. The body cavity of *Amphioxus* is a true coelom lined by mesoderm. It is fairly spacious in the posterior part of the body lodging the mid and hind-gut regions of the alimentary canal, which are suspended by a **mesentery**, as in other vertebrates. In the pharyngeal region, however, the coelom in adult condition is restricted to only a pair of **dorsal longitudinal canals**, a **midventral canal** (**sub-endostylar coelom**), and the vertically running **coelomic spaces** (Fig. 1.48) in the primary gill-bars. These spaces naturally connect the dorsal and the subendostylar coelomic spaces.

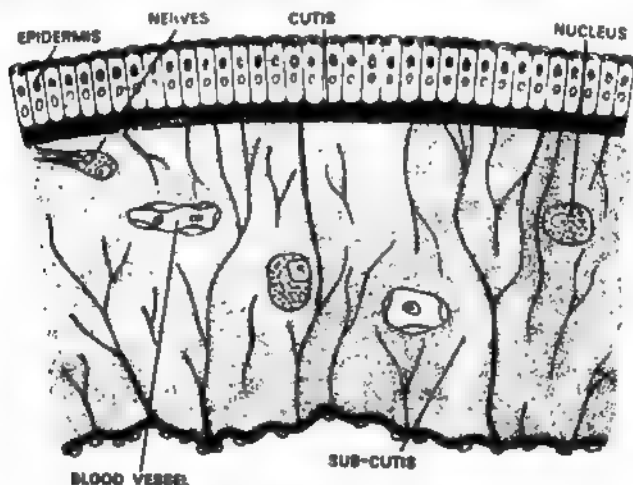


Fig. 1.44. Section of the skin of *Amphioxus* (after Krause).

In the larval forms the coelom in the pharyngeal region is uniform and surrounds the pharynx. As the development proceeds it becomes restricted because the gill-slits arise as outgrowth of the pharynx which meet and fuse with corresponding inpushings of the body wall of that region. At the point of fusion a perforation appears on each such formation, placing the pharynx in communication with the outside. As a result of these changes the coelom is obliterated except in the dorsal and ventral regions and in the septa (primary gill-bars) between the gill-openings. The coelom is further reduced in higher chordates in which it is completely absent from the pharyngeal region.

Alimentary Canal. The alimentary canal is a perfectly straight tube lined throughout by ciliated epithelium. It begins at the **mouth** which is situated at the base of the buccal funnel. The mouth itself is guarded by a ring of sphincter muscles bearing numerous slender sensory velar tentacles, which normally project backwards into the pharynx.

The velum leads into a wide chamber, the **pharynx** or **branchial sac**, where the main operation of food collection is performed. The pharynx is flattened from side to side and possesses a large number (about 200) of oblique vertical slits, the **gill-clefts**. The number of gill-clefts increases with age, the new ones being added constantly at the

THE PROTOCHORDATA

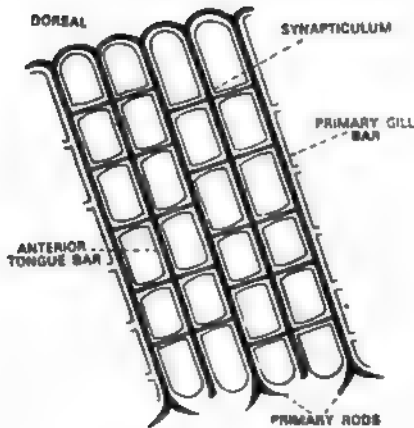


Fig. 1.45. Skeletal elements of the pharynx.

posterior end of the pharynx. The partitions between the adjacent gill-clefts are supported by diagonally sloping skeletal rods called gill-bars, which are of two types, the **primary** with forked ends, and the **secondary** with unforked ends. Both these alternate regularly along the length of the pharynx and differ not only in their structure, but also in their mode of development. The secondary bars do not exist in the earlier stages, but they grow down secondarily from the upper wall of the cleft, dividing the primary gill-cleft into two, and fuse with the ventral wall. All the forked bars are connected by cross bars of **synapticulae**, that run right across the gill-openings. The primary and secondary bars are traversed by blood vessels. The sides and inner surfaces of the gill-bars are ciliated and are mainly responsible for creating currents driving the water outwards through the slits, thereby drawing a feeding current of water in at the mouth. In the floor of the pharynx lies the **endostyle** comprising four columns of mucous-secreting cells that produce sticky threads in which food particles become entangled. On the dorsal surface of the pharynx there is a median **epipharyngeal groove**, which also assists in food catching. Behind the velum lie certain ciliated **peripharyngeal tracts**, which divert the food particles captured by the sticky threads of the endostyle to the epipharyngeal groove in which they are conducted backwards to the mid-gut.

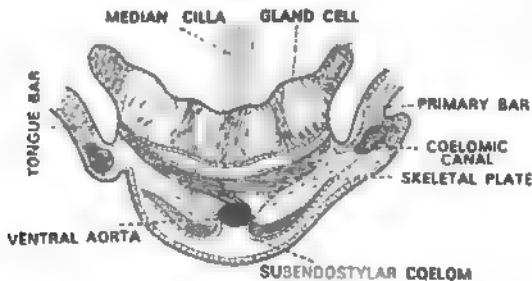


Fig. 1.46. Transverse section of the endostyle

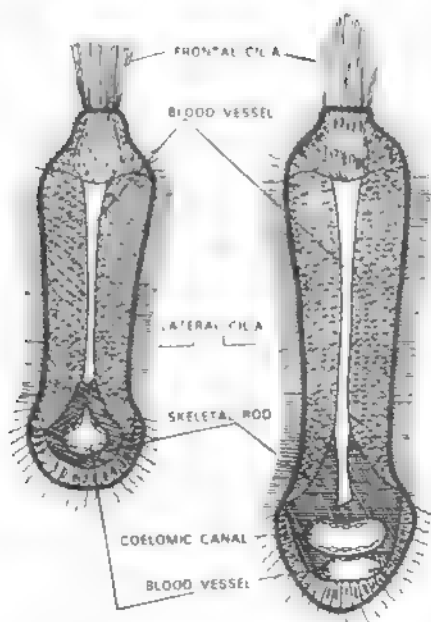


Fig. 1.47. A, transverse section of secondary gill-bar and B, transverse section of primary gill-bar

Atrium. The entire branchial apparatus of the adult, *Amphioxus* is surrounded by a large water-filled chamber called the atrium. The atrium is a peripharyngeal cavity of secondary origin and opens to the exterior by a small posteriorly directed aperture called the **atriopore**, situated on the ventral side of the body just in front of the ventral fin, and carries out the water that comes through the pharyngeal clefts. The atrium is lined by ectoderm, for it arises as long ectodermal folds of the body wall called the **metapleural folds**, which are united ventrally by a transverse shelf, the **epipleur**, enclosing an atrial cavity surrounding the branchial apparatus and the anterior part of the intestine. The metapleural folds thus form the atrium, and extend ventrally beyond it as permanent extension which serve as a pair of bilge keels, undoubtedly stabilizing the animal to some degree while it is swimming. At the level of the posterior end of the pharynx the atrium gives rise to two forwardly directed pockets, one on each side, pushing into the dorsal coelomic canal, with which it is reported to communicate. These pockets are called the **brown funnels** and are of unknown function. The atrium is a protective structure. It protects the delicate pharynx while the animal is in its sandy burrow and helps to maintain an uninterrupted current of water.

The pharynx projects freely into the atrium being surrounded by the continuous atrial cavity at the sides and below, but dorsally it is held in position in two ways. First, its dorsal wall (which is grooved to form the **hyperpharyngeal groove**) is closely adherent to the sheath of the notochord, and secondly, the pharynx is attached through the intermediation of the primary bars. These are suspended to the muscular body wall by a double membrane, called the **ligamentum denticulatum**, which forms at once the roof of the atrial chamber and the floor of a persistent portion of the original body cavity or coelom (the dorsal coelomic canal on each side of the pharynx). Thus the ligamentum denticulatum is lined on one side by the ectodermal atrial epithelium,

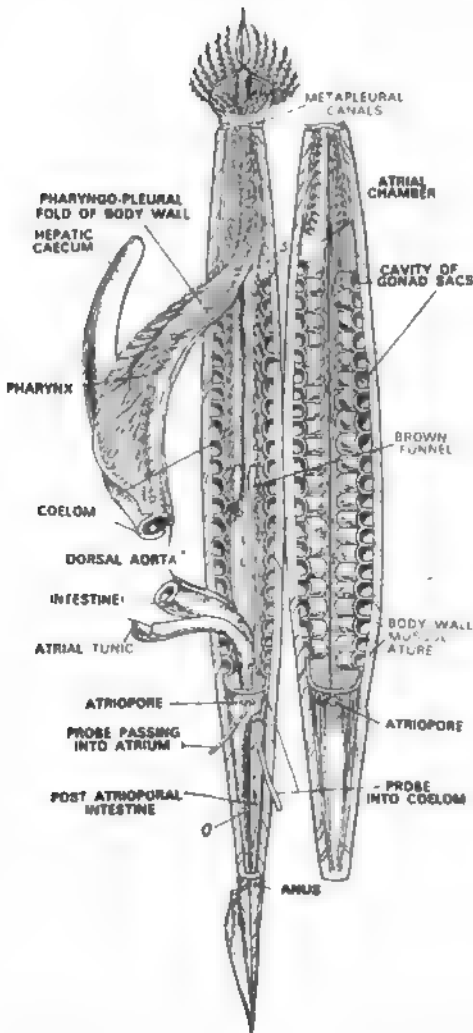


Fig. 1.48. Dissection of *Amphioxus* to show the internal anatomy

and on the other by the mesodermal coelomic epithelium. Now this ligament is inserted into the primary bars some distance below the upper limits of the gill clefts, and it, therefore, follows that corresponding with each tongue bar, the atrial cavity is produced upward beyond the insertion of the ligament into a series of bags or pockets which may be called **atrial pouches**. At the top of each of these pouches there is a

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minute orifice, the aperture of a small tubule (nephridia) lying above each pouch in the dorsal coelom.

The pharynx opens behind into the **mid-gut**¹ which narrows posteriorly and gives a ventral diverticulum, often called **liver**. It lies rather to the right side of the pharynx, and secretes digestive enzymes (Barrington). Actually the food does not pass into the

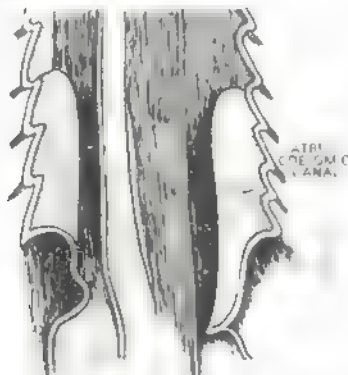


Fig. 1.49. A portion of the above enlarged to show the atrio-coelomic canals.

diverticulum as was formerly believed. The **mid-gut** runs straight posteriorly as the **hind-gut** or **intestine** and opens at the **anus**. The hind end of the mid-gut is marked by a specially ciliated region, the **ilio-colon ring** whose cilia rotate the food and mucous as it passes. In the mid-gut extra cellular digestion takes place. Absorption takes place in the intestine and partly also in the mid-gut, probably by intra-cellular digestion. The faeces is discharged through the anus.

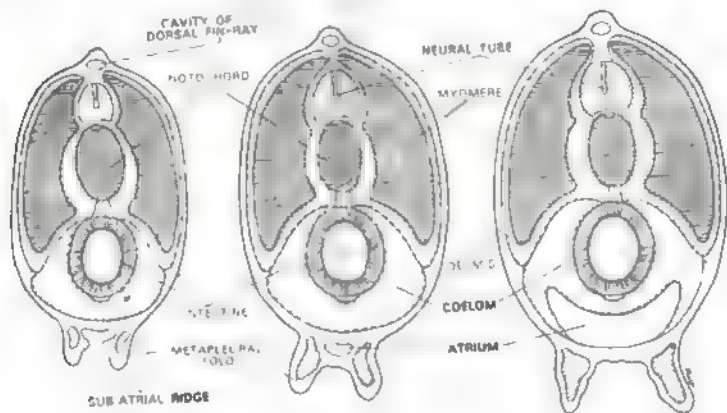


Fig. 1.50. Formation of the atrium.

¹Called stomach by many but as it contains no gastric glands the name midgut is preferred here.

Feeding. *Amphioxus* feeds upon minute organic particles chiefly microscopic animals and plants, which it strains off from the surrounding seawater by the automatic filtering action of the pharynx. It does not move about in search of food. The

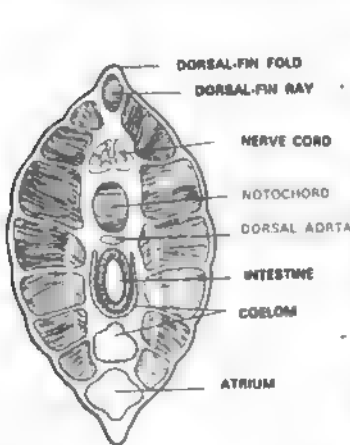


Fig. 1.51. Transverse section of *Amphioxus* showing atrium and coelom.

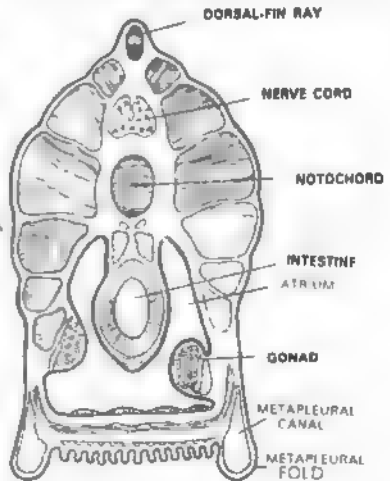


Fig. 1.52. Transverse section of *Amphioxus* showing atrium in the region of gonads.

water is constantly entering the mouth and passing out in the atrium through the gill-slits, it is expelled at the atropore. This food-bringing water current is produced and maintained by the action of cilia, that is why the animal is described as a ciliary feeder.

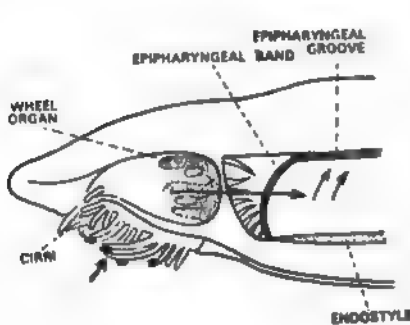


Fig. 1.53. Feeding currents in *Amphioxus*, main current indicated by large arrow and subsidiary currents by small arrows (after Orton).

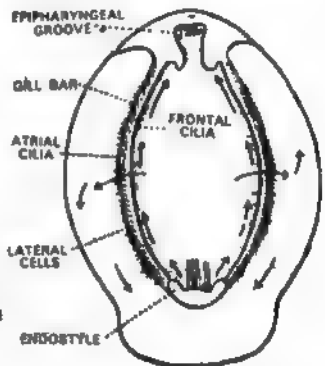


Fig. 1.54. The direction of feeding currents shown in a diagrammatic transverse section of *Amphioxus* (after Orton).

This complicated mode of feeding is extremely interesting and resembles that of the ascidians and also resembles, to some extent, that of the *Ammocoete* larva of the lamprey eel. The difference is that in the *ammocoete* the current is produced by muscular movements of the wall of the pharynx and velum. The ciliary mode of feeding is believed to be primitive and it is assumed that the primitive chordates employed similar method for feeding.

The anterior and posterior faces of each gill-bar are covered with long powerful cilia, the **lateral cilia** (Fig. 1.54). The lashing movements of these drive water out of the pharynx through the gill-slits into the atrium. This exerts a pull on the water which is drawn in at the mouth (Fig. 1.53). This water current is further strengthened by the cilia of the atrial epithelium on the outer face of the gill-bars and isolated patches of ciliated tissue overlying the gonads. The current carries the particles suspended in it backwards and outwards from the mid-line towards the gill-bars. This current is directed upwards from the ventral towards the dorsal mid-line by the lashing of the cilia (**frontal cilia**) on the inner (pharyngeal) surface of the gill-bars.

The gland cells of the endostyle (Fig. 1.53, 1.54) secrete mucous. The median tract of the long endostylar cilia drive this mucous to the lateral endostylar cilia. This mucous is transferred to the side walls of the pharynx by the lateral tracts of cilia. The course of the mucous ascending the walls of the pharynx is not definitely ventro-dorsal but somewhat oblique because the main food bringing current takes it in a backward direction. From the epipharyngeal groove the mucous is carried back to the opening of the oesophagus.

From the foregoing it is evident that a water current is automatically maintained by the action of the cilia on the sides of the gill-bars (**lateral cilia**). The ciliated structures in front of the velum and the peripharyngeal bands play only a subsidiary part. The water current enters the pharynx and passes out into the atrium through the gill-slits. Particles of suspended matter are forced against the pharyngeal surfaces of the gill bars and get entangled in the mucous, which lies between the bases of the cilia. The food particles would be washed away if the thin sheet of mucous on the walls of the pharynx were lacking. The food particles entrapped by the mucous move dorsally to the epipharyngeal groove. The cilia of the epipharyngeal groove carry the food stream back to the oesophagus.



Fig. 1.55. A portion of the gill-bar and the currents along it as seen from the anterior surface

The buccal cirri are folded over one another to form a mesh for straining the larger particles during feeding. Such particles accumulate progressively on the cirri and a stage comes when they prevent a water current from entering in. To remove these accumulated particles a violent current of water is produced by the muscular movement of the floor of the pharynx. The atriopore is closed at the same time and the atrial floor is suddenly raised, reducing the volume of the atrial cavity and forcing a powerful current of water into the oral cavity through the pharynx. The cirri are also flexed in and out of the oral hood to dislodge the particles on them.

In spite of the water current some particles may drop in the buccal floor. These are driven away by the ciliary current produced by the wheel organ. Likewise some heavy particles (with higher specific gravity) may fall into the extreme anterior part of the pharynx (where gill-slits are absent) but they are picked up and passed on to the

epipharyngeal groove by the peripharyngeal bands.

The food-laden mucous is carried down the gut by ciliary action, that is why the entire gut including the mid-gut diverticulum is ciliated. The food rolls up with mucous to form a cord by the time it enters the oesophagus. This food cord is rotated as it passes slowly backwards in the gut. The rotation is brought about solely by the action of ciliated cells in the ilio-colonic ring, and behind this region. Any portions which break away from the cord fail to rotate behind this region. The chief ciliated tracts here include a lateral tract on the left hand side of the anterior part of the mid-gut; a dorsal tract which links up with the lateral tract in the posterior part of the mid-gut and a dorsal tract in the hind-gut.

Physiology of Digestion. The lining epithelium of the gut also possesses rich gland cells secreting digestive juices. All the regions of the gut behind the oesophagus produce their own secretions, those of the mid-gut diverticulum are driven out into the gut by ciliary actions. The food passing through the gut mixes with these secretions which bring out digestion, which starts in the mid-gut with the addition of the first instalment of digestive juices and continues till the gut contents pass out. In addition to the extracellular digestion, it is quite likely, that intracellular digestion also takes place. Some of the cells of the lining membrane of the gut pick up small particles of food that are digested within them. This process most probably is restricted to the region of the hind-gut. The digested food is absorbed to some extent by the mid-gut but mainly by the hind-gut.

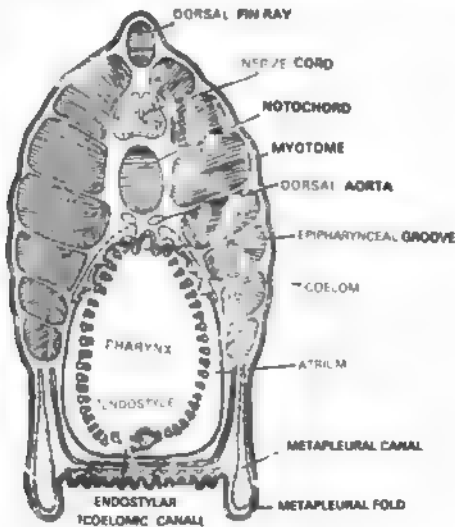


Fig. 1.56. Transverse section of *Amphioxus* through the region of the pharynx.

Gaseous Exchange. The pharynx of *Amphioxus* is mainly a feeding organ. It is assumed, however, that some gaseous interchange between the blood and sea water takes place in the pharynx. No experimental evidence supports this view. Further, it has been suggested that the exchange of gases takes place through the whole surface of the body. The walls of the atrium are particularly believed to do this work.

Skeletal System. The skeletal system of *Amphioxus* comprises (i) the notochord, (ii) the cartilaginous support of the oral hood, (iii) the gill-bars of the pharynx and (iv) the fin-rays. The notochord of *Amphioxus* extends from the very tip of the head to the end

of the tail, projecting beyond the level of myotomes. This is probably related with the burrowing habit of the animal. The notochord of *Amphioxus* is complex in structure. It is surrounded by a thick fibrous non-cellular sheath, the **notochordal sheath**. The chord proper consists of large vacuolated cells¹ filled with fluid. It is the turgour pressure of these cells acting against the resistance of the notochordal sheath that gives to the notochord its stiff elastic nature and enables it to function as the main axial skeleton of the body. The oral hood is supported by a thin ring of cartilage, the **cartilaginous loop**, around its edges which protect the opening from collapse. Similar skeletal rods occur in the cirri and articulate with the cartilaginous loop in the oral hood. These skeletal pieces are made up of similar tissue as forms the notochord and have large vacuolated cells. The gill-bars have already been described. The median ridges are supported by **fin-ray boxes** made up of connective tissue, each of which contains a gelatinous substance. The dorsal fin has a single row of such boxes, whilst the ventral has a double, right and left, row of the fin-ray boxes.

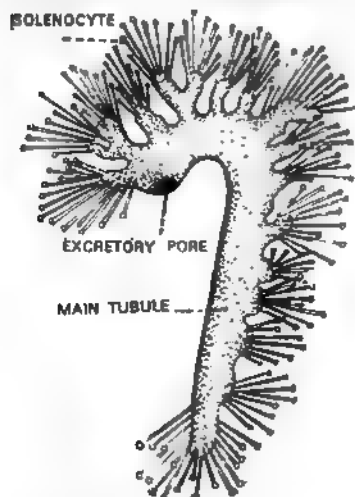


Fig. 1.57. Nephridium of *Amphioxus* (after Goodrich).

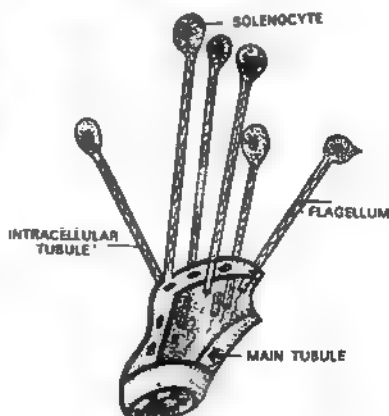


Fig. 1.58. A portion of nephridium magnified and tubule cut open (after Goodrich).

Excretory System. The excretory system of *Amphioxus* does not agree with the basic chordate plan. It consists of **protonephridia** as found in many invertebrates such as the platyhelminths, annelids, branchiopods, etc. There are ninety pairs of nephridia lying above the pharynx, each pair of nephridium is a small bent tube (Fig. 1.57) consisting of a **horizontal** and a **vertical** sac. The horizontal limb is situated in the coelom and opens into the atrium, at the excretory pore on the dorsal edge of the gill-slit, while the other limb passes ventrally in the atrium and terminates blindly (Fig. 1.57). The coelomic portion is studded with numerous elongated **solenocytes** or **flame cells** (Fig. 1.58). Each solenocyte is an elongated cell with nucleus and a long flagellum that is constantly moving like a flickering flame. The tufts of solenocytes project into

¹ According to Young the chord consists of a series of flattened plates arranged with their flat surfaces in the transverse plane of the body. The plates are of two types, fibrous and homogeneous which alternate with each other. Each plate develops as a highly vacuolated cell, the nuclei being pushed aside to the dorsal and ventral edges.

the dorsal coelomic canal and owing to the breaking down of the coelomic epithelium immediately above them, they become directly bathed in the coelomic fluid, a factor which, no doubt, facilitates the extraction of nitrogenous waste.

The flame-cells do not open internally, but are in close contact with special blood vessels (*glomeruli*) whose walls separate the flame-cell from the coelomic epithelium. Bulk of nitrogenous excretion is carried out by nephridia. The excretory material in the coelomic fluid diffuses through the wall of the flame cell, is driven into the body of the nephridium by the flagellum and finally reaches the atrium, whence it moves out through the atriopore. Probably the nephridia function as the protonephridia of non-chordates and also act as osmoregulators of the body.

In addition to the paired nephridia, a single large nephridium of Hatschek, occurs above the roof of the pharynx laterally to the left dorsal blood-vessel. It resembles the paired nephridia in structure. It is a narrow tube which opens at its posterior end into the pharynx just behind the velum, and then passes anteriorly to end blindly just in front of Hatschek's pit. It receives several solenocytes along its length and they are associated with a network of capillaries. The nephridia of *Amphioxus* are derived from ectodermal layer of the embryo as such they resemble those of non-chordates both developmentally as well as structurally.

Excretory function is also attributed to the numerous renal papillae, found in the floor of the atrium. But this is not supported by experimental evidence.

Circulatory System. The circulatory system of *Amphioxus* appears peculiar in that it has no heart and the blood contains neither haemoglobin nor other respiratory pigment. All the same it presents the fundamental plan on which the circulation of other chordates is based. The circulation is brought about by slow waves of contraction that pass along the major arterial vessels in such a way that the blood is driven forwards in the ventral vessel and backwards in the dorsal. Just below the hinder end of the pharynx lies a large sac, the sinus venosus, that receives blood from all parts of the body. From this arises a large branchial artery, the ventral aorta (*truncus arteriosus*) and proceeds forwards in the ventral wall of the pharynx below the endostyle. It is contractile and drives the blood forwards. From the ventral aorta spring several vessels, the afferent branchial arteries, on each side with small contractile dilations at their bases, presumably acting as branchial hearts. The afferent vessels pass up the primary branchial lamellae and communicate by cross branches with similar vessels in secondaries or tongue lamellae. While traversing these vessels the blood is exposed to the aerating influence of the respiratory current and leaves the branchial lamellae dorsally by efferent branchial arteries, which on each side, open into paired longitudinal vessels the right and left dorsal aortae, lying one on either side of the epipharyngeal groove. Anteriorly both the aortae are continued forward to the region of the snout, the right being relatively delicate. Posteriorly they unite behind the pharynx to form a single dorsal aorta (Fig. 1.59). From the aortae blood is carried to a system of lacunae which supply the tissues. There are no true capillaries.

From the lacunae the blood is collected into veins, the most important of which are the caudal, cardinals and a plexus on the gut. There are two pairs of cardinals, the anterior cardinals and the posterior cardinals, running in the dorsal wall of the coelom, collecting blood from the muscles and body wall. They open into the sinus venosus by a pair of vessels, *ductus Cuvieri*, which pass ventrally and across the coelom to join the sinus venosus on the floor of the gut. The caudal veins join the plexus on the gut from which blood is collected by a large median subintestinal vein running on to the liver. The blood in this flows forward and at the origin of the liver it passes insensibly into a hepatic portal vein, which extends along the ventral side of the liver and breaks up into capillaries in that organ. From the liver blood makes its way into a hepatic vein which extends along the dorsal side of the digestive gland and turning downwards and forwards joins the sinus venosus. All the blood from the intestine has to pass through the liver before reaching the sinus venosus, hence it is said to constitute the hepatic portal system.

Nervous System. The nervous system consists of a central nervous system, which is hollow, tubular situated on the dorsal side of the notochord, and fine nerves arise from

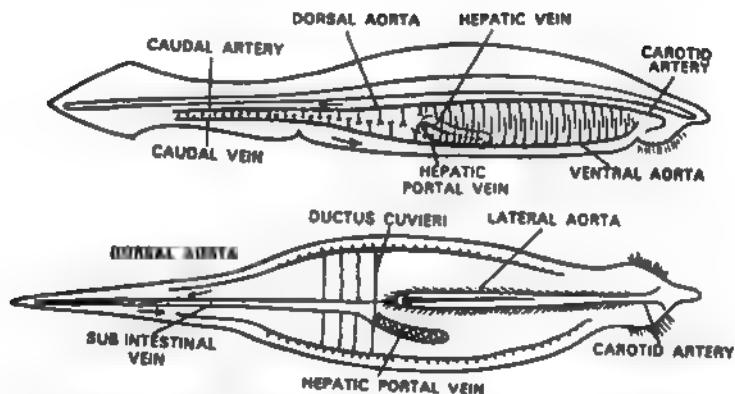


Fig. 1.59. Circulatory system of *Amphioxus*. A, side view of the main vessels (without 'cardinal veins'); B, dorsal view of main vessels (ventral aorta omitted).

it forming the **peripheral nervous system**. The nerve cord is like that of other vertebrates but it tapers anteriorly (Fig. 1.60) and is broad at the posterior end. Apparently the anterior end does not show any enlargement to form an elaborate brain, but some people contend that the **central canal**, running across the centre of the cord, is enlarged at the anteriorend to form **cerebral vesicles** (Fig. 1.61). The nerves connected to the periphery arise by two simple sets of nerve roots, a **dorsal** and a **ventral** but the roots do not join. The ventral roots (Fig. 1.60) lie opposite the myotomes, to which they carry motor (or efferent) fibres, and these end on the muscle fibres with motor end-plates as found in the vertebrates. The dorsal root runs out between the myotomes and carries all the sensory (or afferent) fibres of the segment and motor fibres of the non-myotomal muscles of the ventral part of the body. This pattern of nerve arrangement conforms with that of other vertebrates. As in vertebrates there are motor nerve cells forming a plexus in the gut wall. The fibres of the peripheral nerves differ from those of vertebrates in that they have no thick myelin sheath. The sensory fibres are more like the neuro-sensory cells of the invertebrates. The cell bodies are not collected into

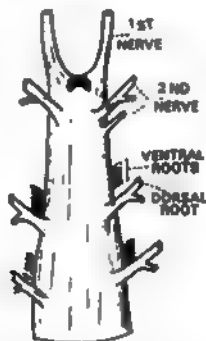


Fig. 1.60. Anterior part of the central nervous system of *Amphioxus*.

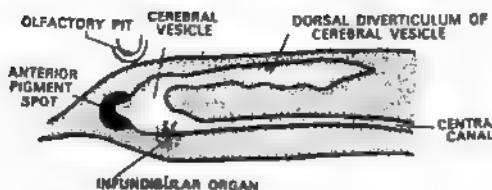


Fig. 1.61. Vertical section of the anterior part of the neural tube of *Amphioxus* (modified after Bocke).

spinal ganglia but lie either close below the epidermis or scattered along the course. The spinal cord has a narrow lumen and its elements are arranged as in other vertebrates.

Organs of Special Sense. The infundibular organ, probably, gravity or pressure receptor, is situated in the wall of the cerebral vesicle. It is composed of tall cells with long cilia that beat in opposite direction to those of the rest of the vesicle. The Kolliker's pit (the so-called **Olfactory pit**), presumably a chemoreceptor, is situated at the anterior end of the nerve cord. In young stages cerebral vesicle opens by an anterior neuropore which closes later. At the place of closure develops a pit of skin lined by special epithelium supplied with nerve endings. This is the Kolliker's pit. The tentacles and oral hood are also provided with chemoreceptors, usually grouped in papillae on the oral curri and on the velar tentacles.

Certain **photoreceptors** occur along the walls of the central canal of the neural tube and in definite lateral tracts. In the anterior third of the body they are also found in the ventral wall of the neural tube. They occur along the whole length of the neural tube. These pigmented photoreceptors have been called **eye spots** or **simple eyes**, and resemble those of the planarians. Each eye-spot (Fig. 1.61) consists of a single large cell

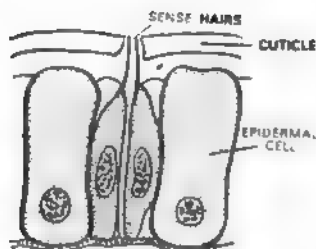


Fig. 1.62. Sense cells of the epidermis of the dorsal in (redrawn after Joseph).

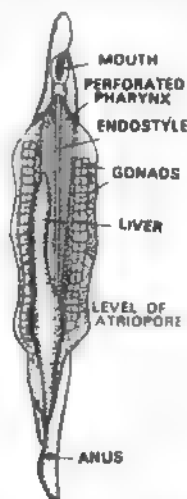


Fig. 1.63. *Amphioxus* cut open ventrally to show the position of gonads (after Rathke). Mouth appearing as an elongated slit when relaxed (as in the lamprey.).

bearing a cap of blackish-brown pigment in a cupshaped area to one side of the cell. Between the pigment cup and the nucleus the cytoplasm is differentiated to form a striated layer which probably acts like a lens. A single nerve fibre leaves the cell on the side opposite to that bearing the pigment cup.

It is evident that *Amphioxus* is provided with sensory and motor systems that serve to keep it in its sedentary position and enable it to collect food from the currents produced by the cilia. Kolliker's pit, the chemoreceptors of the tentacles, and oral hood and infundibular organ perhaps provide it with mechanisms which help it to make appropriate movements of life such as swimming, burrowing, closing the oral hood and escape, etc.

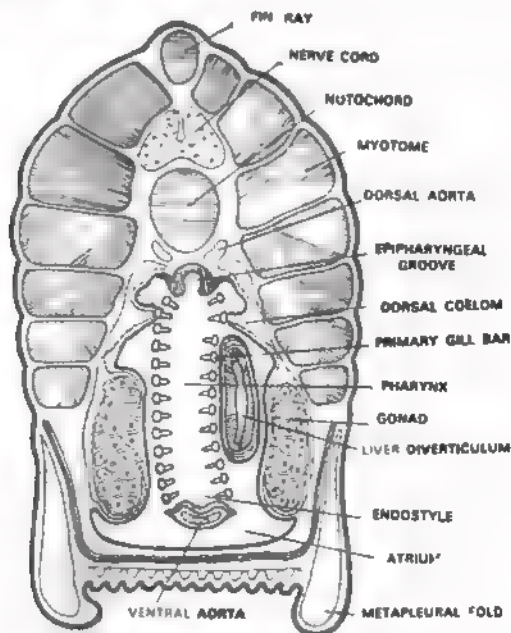


Fig. 1.64. Cross-section of *Amphioxus* showing gonads.

Reproductive System. The sexes are separate, but on the basis of gonads the males and females cannot be distinguished. The gonads of *Amphioxus* are hollow sacs laying in the anterior two-third of the body on the ventral side. They are arranged strictly metamerically, one pair in each of the segments twenty-five to fifty one. They appear as a series of bulges inwards towards the atrium (Fig. 1.63). The gonads are without ducts. When mature the overlying tissue ruptures allowing the release of the sex-cells in the atrium, whence they pass out through the atriopore. After the escape of the sex-cells the aperture in the tissue closes.

The germ-cells arise as proliferations of the coelomic epithelium but the relation of the gonad with the coelom in the adult is not clear. In the larva after the separation of the dorsal metamERICALLY segmented blocks of mesoderm differentiate into the myotomes, sclerotomes and dermatomes. Of these the first gives rise to the segmental muscles while the latter two form the connective tissues. For some time the somites retain a narrow cavity, which is coelomic in nature as it was continuous with the perivisceral coelom at an early stage. The germ-cells develop from the ventral wall of

this cavity. This tissue is called **gonotome** (Fig. 1.65) and is quite distinct from the embryonic muscular tissue.

The gonotomes form small buds which grow out forward and ventralwards. The buds remain connected to the somites for some time, but separate later establishing young independent gonads. Then each gonad acquires a **primary gonadal cavity** (Fig. 1.65) and as it grows further it becomes completely surrounded by a **secondary or perigonadal cavity** (called **gonocoel** by some). The gonocoel (Fig. 1.65) is lined by tissues derived from the wall of the somite into which the gonad bulges. In the primary gonadal cavity the germ cells are budded off from the cells forming the outer (atrial) wall. The walls of the secondary gonadal cavity separate the germ-cell producing tissue from the atrial epithelium. On the inner surface of the gonad lies a layer of **follicular epithelium**, itself derived from the cells of the wall of the primary gonadal cavity. The germ-cells and the follicular epithelium is separated by a large blood sinus that opens into the postcardinal vein.

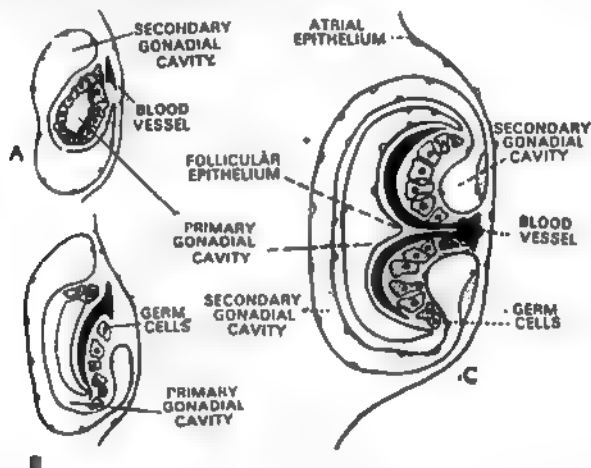


Fig. 1.65. A, B, Development of gonads; C, Vertical section of an older gonad (based on Cerfontaine).

Development. The eggs escape from the gonads through two slit-like openings into the atrium, whence they pass out through the atriopore into the sea where fertilization occurs. The egg is **microlecithal**, i.e., contains a relatively small quantity of yolk. The first **polar body** separates and comes to lie just outside the **vitelline membrane** by the time the egg reaches the sea. The cytoplasm of the egg is arranged into two layers (i) a **peripheral layer**, free from yolk; lying just below the vitelline membrane; (ii) a mass of yolky cytoplasm which lies mainly towards the vegetative pole of the egg, because a considerable part of the animal pole is occupied by the **egg nucleus** (germinal vesicle). The animal pole of the egg gives rise to the future antero-ventral part, whereas, the vegetative pole corresponds with the postero-dorsal part of the embryo.

The sperm enters the egg near the vegetative pole and this stimulates maturation of the egg, as only after this happens, the second polar body is given off and comes to lie near the animal pole just within the vitelline membrane. The zygote nucleus is formed in the usual way and lies nearer the centre of the egg than was the nucleus of the unfertilized egg.

Following fertilization the cytoplasmic contents are completely rearranged. As a result of the rupture of the germinal vesicle an area of clear cytoplasm is left there almost in contact with the peripheral layer. Later this flows towards the vegetative

pole and ultimately condenses to form a crescent-shaped structure at the future posterior end. The arms of the crescent reach round the sides of the egg and partially embrace the yolky-area so that the egg is now bilaterally symmetrical with respect to the axis of the egg. It has been determined that the various cytoplasmic areas give rise to definite structures in the embryo, and if any area is removed or damaged its correlated structure may not be formed. The different areas of cytoplasm have, therefore, been termed the **organ-specific areas** or (**organ forming substances**), and because this regional differentiation results in a definite organ pattern being recognizable in the egg it is said to be the **mosaic type**. The material of organ-specific areas becomes distributed in an orderly fashion to various blastomeres as the cleavage (determinate cleavage) proceeds. It has been proved that the clear cytoplasm in the animal half gives rise to the **ectoderm**, the **endoderm** is formed by the yolky cytoplasm, whereas the **mesoderm** is formed by the crescent of granular cytoplasm.

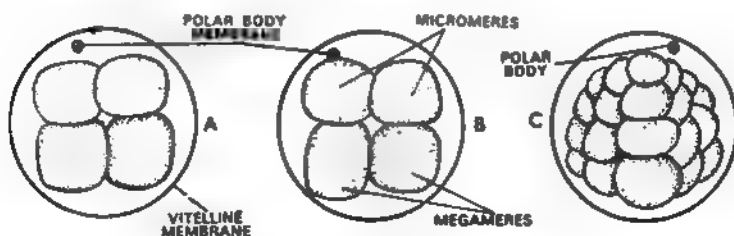


Fig. 1.66. Early cleavages in the egg of *Amphioxus*.

Cleavage. The fertilized egg begins to segment at once. The cleavage is **holoblastic**, i.e., the egg is completely divided into separate blastomeres. The first cleavage furrow lies vertical (Fig. 1.66) and divides the whole egg including the mesodermal crescent into two halves, representing the right and left halves of the embryo. The second cleavage is also vertical, at right angles to the first. The third cleavage passes through just above the equator dividing the four blastomeres into an upper tier of four smaller cells (**micromeres**), and a lower tier of four larger cells (**megameres**). In attaining the sixteen cell stage each of the blastomeres divides by meridional furrow forming eight micromeres and eight megameres. Each cell then divides into upper and lower halves in the fifth cleavage resulting in the formation of eight tiers of four cells each. At the sixth cleavage the planes are oblique producing a sixty-four cell embryo. After this the cleavages become somewhat irregular and the cells tend to flatten out against each other. The cleavages continue till a somewhat spherical **blastula** is formed. It is rather pear-shaped when viewed from the side, the pointed end being posterior. The **blastocoel** (Fig. 1.67) is a distinctive cavity in the centre of the group of blastomeres, filled with fluid. During early cleavages a jelly-like substance accumulates between the dividing blastomeres. This jelly-like substance later absorbs water and becomes fluid as the divisions proceed. In the fully formed blastula the blastocoel becomes a spacious fluid-filled cavity.

In the next stage the blastula flattens on one side and becomes hemispherical. Its walls show areas of histologically distinct cells as a result of the orderly distribution of the organ-forming substances. The bulk of the ventral half of the blastula (flat surface) is occupied by columnar cells of the **ectoderm**. The endoderm forming larger yolky cells form a plate-like area across the dorsal part of the blastula. The cells of the mesodermal crescent become smaller and bind the endodermal plate on its sides and posterior borders. A close examination reveals a small area of slightly smaller notochord forming **chorda cells** immediately anterior to the endodermal plate. Specialised ectoderm cells destined to form the neural plate can also be made out in front of the chorda cells.

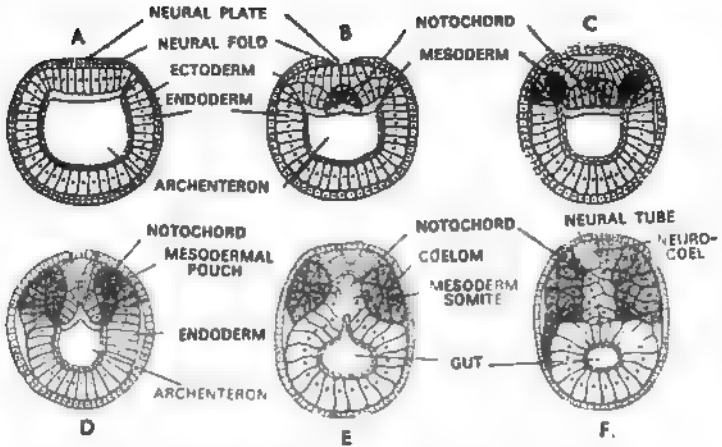


Fig. 1.67. Further stages in the development of *Amphioxus*.

mal plate. The flattening becomes more and more pronounced and ultimately the endodermal plate becomes concave (Fig. 1.67) and sinks inwards as if pushed in by some invisible finger. The blastocoel is gradually reduced in size. Finally, the embryo becomes cup-shaped, the cavity of the cup being the archenteron (Fig. 1.67C), its opening the blastopore (which later becomes anus) and its rim the lips of the blastopore. At this stage the dorsal lip is really in an anterior position and contains the chorda cells. The lateral lips and the ventral lip are formed by the cells of mesodermal crescent. The arms of the mesodermal crescent come to form groove-like areas of rapidly dividing cells (mesodermal grooves) which run in the lateral walls of the archenteron from the lateral lips of the blastopore. The middle of the mesodermal crescent still remains in the ventral lip of the blastopore. At about this stage the gastrula becomes covered with flagella by which it rotates in the egg case.

The embryo now elongates and its dorsal side flattens. The blastopore becomes smaller in size and shifts from a nearly dorsal to a posterior position by the backward growth of the dorsal lip.

The rudiment of first definite organs now appears. This is the formation of the

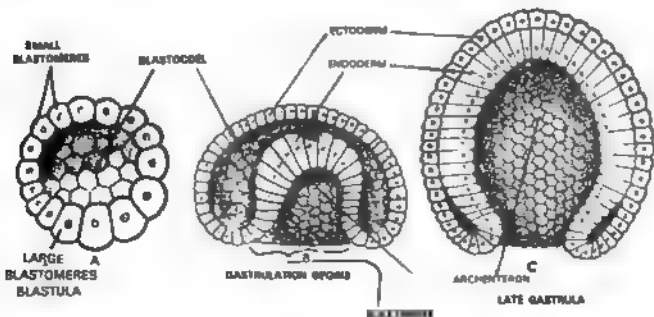


Fig. 1.68. Gastrulation. A. the blastula, B. early gastrula, and C. later gastrula.

neural plate, the first organ to appear in all higher vertebrates. A strip of ectoderm cell in the mid-dorsal line becomes larger, and cells become columnar and the whole surface becomes slightly flattened. This is the neural plate. As growth proceeds the plate sinks inwards and the ectoderm at the sides rises to form **neural folds**. The two folds originate at the sides of the blastopore and, beginning at the posterior end, they grow towards each other, finally meeting in the mid-dorsal line. As the ectodermal roof is being formed in this way the edges of the neural folds also start growing towards each other ultimately rolling up to form the **neural tube**. Since the neural folds extend laterally to the blastopore, when they meet, or the blastopore becomes roofed over by them, and this means that at this stage the neural tube communicates by a short tube with the hinder end of the archenteron. This short tube is known as the **neurenteric canal**. Soon after this the blastopore is closed and the neurenteric canal is interrupted.

It is evident from the above that the neural tube formation in *Amphioxus* is different from that of other vertebrates in that (i) the neural plate sinks inwards before rolling up; (ii) the neural folds merely roof over the plate and do not contribute to the formation of the neural tube, and (iii) the neural folds make their first appearance at the posterior end.

As soon as the blastopore is closed the chorda cells, which got invaginated as a strip forming the mid-dorsal part of the archenteric wall, rearrange themselves forming the **notochord**, which, in the earliest stages, is made up of a single row of disc-shaped cells. Later on these cells become vacuolated and a notochord sheath invests them.

As mentioned earlier the dorso-lateral wall of the gut consists of the mesodermal grooves which by now become metamerically segmented into **mesodermal pouches** by the development of transverse partitions. These make their appearance anteriorly and proceed, with growth, to the posterior end of the body. As growth proceeds, beginning at the anterior end, the mesodermal pouches become cut off from the wall of the archenteron and finally the openings by which mesodermal pouches communicated with the archenteric cavity close up, forming a series of closed **mesodermal sacs** each enclosing a small cavity. These occupy the space between the ectoderm and endoderm on each side of the gut rudiment. Soon after the formation of the mesodermal sac an extremely rapid growth in the length of the embryo sets in and then hatching takes place, the minute larva swimming around by the aid of cilia, but it is incapable of feeding as the mouth and anus are not yet formed.

The small cavities between the mesodermal sacs now enlarge and each sac grows ventralwards, and finally, the ventral wall of each member of a pair (right and left) meets in the mid-ventral line. At the next stage the walls separating the right from left sacs in the mid-ventral line fuse and disappear with the result that the right and left cavities run into each other. Later on the metamerism of the mesodermal pouches is lost with the disappearance of cross partitions establishing a cavity, the **splanchnocoel**, continuous throughout the length of the embryo extending around the ventral and lateral parts of the gut. At about the level of the ventral surface of the notochord a horizontal partition is formed in each mesodermal sac separating it into a dorsal and a ventral portion. The dorsal portion is distinguished as the somite (*epimere*) and its cavity is the **myocoel**; whereas the ventral section called the lateral plate and its cavity form a part of the coelom. The dorsal parts of the mesoderm thus retain their metamerism and form structures which correspond to the somites of vertebrates.

The larva keeps on swimming without feeding for some time and elongates rapidly. Then mouth develops. A patch of ectoderm fuses with the endoderm of the gut on the left side of the ventral surface of the head and then perforation occurs at this point.¹ This is the mouth, which has ciliated borders. The anus is formed in a similar manner on the left of the mid-ventral line near the posterior part of the body.

From now onwards the development is markedly asymmetrical, presumably in connection with the spiral movement and method of feeding. The first two coelomic pouches also grow asymmetrically, the right one grows large and becomes the preoral body cavity or the cavity of the head and the left becomes a rudimentary structure, the preoral pit (Hatchek's pit).

Simultaneously with these changes the pharynx becomes enlarged and gill-clefts also appear. But the gill-clefts do not appear in a regular sequence from front to rear,

nor are they first arranged in anything approaching bilateral symmetry. The first cleft to be formed arises, before mouth opens, as a diverticulum from the anterior end of the pharynx on the right hand side. Ultimately it develops into the club-shaped gland which opens to the exterior just ventral to the mouth. This gland disappears during metamorphosis. Other gill-slits appear in the mid-ventral line. They are the primary gill-slits, fourteen in all, and later on form the gill-slits of the left side. The first series of slits of the right side are eight in number and are formed on the right side of the pharynx above the fourteen previously formed slits. Thus two linear series of slits are present on the same side of the body, the right. With further growth the slits of the left side then move across the mid-ventral line and take up their definite position. Now, six of them close thus forming eight slits on each side. The gill-slits of both sides then become sub-divided by tongue bars and further slits are added to the hinder end of both series.

Below the opening of the club-shaped gland the walls of the pharynx become modified to form a V-shaped ridge of ciliated cells. This is the endostyle, its cells become glandular later on.

In the older larvae a slight ectodermic thickening along the line of the posterior extension of the first somite on the right side is observable. This is the thickening of the first rudiment of the atrial fold which overhangs the gill-slits. A similar fold is developed on the left side. On the inner face of each fold, i.e. the fold that looks towards its fellow of the opposite side, a longitudinal ridge appears, and the two subatrial ridges meeting and coalescing form a canal immediately below the ventral body wall. This canal is the commencement of the atrium. It is at first quite narrow but gradually extends upwards on each side pushing the coelom dorsally. It is at first open both in front and behind—the posterior opening remains as atriopore.

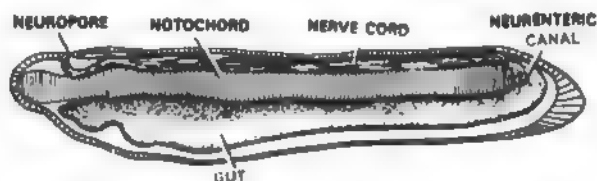


Fig. 1.69. Young *Amphioxus*, soon after hatching

During the larval life the excretory organs are formed. They consist of tubes ending internally in tufts of solenocytes or flame-cells, situated at the lower borders of the primitive gill-slits.

The genital organs arise as small buds of cells which sprout from the anterior angles of the myotomes. They soon become cut off from the myocoel and project into the gonocoel.

The changes which occur during the metamorphosis are: the first gill-slits and the club-shaped gland disappear simultaneously, several of the more posterior primary gill-slits also disappear, a new series of 8 gill-slits make their appearance on the right side above the primitive gill-slits; these new gill-slits—secondary gill-slits—grow downwards pressing the primary gill-slits back to the midventral line and eventually on its left side. Thus, the primary gill-slits, form the adult gill-slits of the left side and secondary gill-slits, those of the right side. In this way the lower borders of the primary gill-slits become the dorsal border, and the excretory organs reach the position in which they are formed in the adult, viz., the dorsal border of each gill-slit. At the same time in both the primary and secondary gill-slits septa grow out and eventually divide each of them into two. These septa are tongue bars. On the dorsal surface of the buccal cavity an extensive series of ciliated grooves make their appearance. These grooves are termed wheel organs. The liver begins as a little ventral pouch of the gut immediately behind the pharynx.

From the above it is evident that some features connected with the method of life of

the larva are all of special interest, especially its asymmetry. The strange sequence of gill formation, the immense left-sided larval mouth, perhaps also the club-shaped gland, are such asymmetrical features of the larva. It is difficult to explain this extraordinary asymmetrical larva of *Amphioxus*, which, nevertheless, becomes metamorphosed into an adult which is nearly bilaterally symmetrical. It must, however, be admitted that the larvae of *Amphioxus* are so extraordinary as to present a serious problem for those who believe that the larval stage represents, in modified form, an ancestral condition of affairs. That a bilaterally symmetrical embryo should pass through an asymmetrical pelagic larval stage in order to attain the form of a practically symmetrical burrowing adult seems to be completely contrary to what should be expected.

But a very plausible solution has been suggested by Stafford. He points out that the ancestor of *Amphioxus* could not have jumped suddenly from a pelagic to a burrowing existence. Some intermediate condition of life must have existed. What was the intermediate state of affairs?

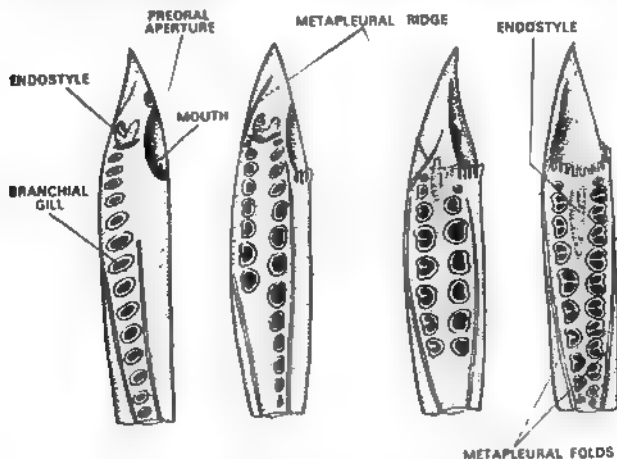


Fig. 170. Larval forms of *Amphioxus* showing changes in the position of gill openings.

In the case of other animals which have deserted a pelagic for a more humble mode of existence there are reasons to believe that a habit of gliding over the surface of the mud preceded a burrowing life. But a ventrally flattened animal like *Amphioxus* could not do this. The moment it ceased swimming it must have tended to fall on one side. This circumstance can actually be observed in the older larvae of *Amphioxus*. Let us assume, therefore, that the ancestors of *Amphioxus*, after deserting their free-swimming life passed through a stage when they lay on their side on the bottom. Under these circumstances it would be an advantage to twist the mouth round to the left side so as to bring it near the detritus which served as food, and to twist both sets of gill-slits round to the upper right side of the body so that the waste matter might be ejected without disturbing the substratum on which the animal is feeding. Similar conditions of life have led to the modern flat fishes to become asymmetrical. They have twisted the mouth down and the eyes round to the upper side of the body.

But if this solution sounds plausible two further questions arise: (a) Why does only one row of gill-slits develop? and (b) Why does the asymmetrical condition appear at the stage of its development when, to judge from its environment, the larva ought to be bilaterally symmetrical?

The answer to the first question has an important bearing on the way in which the

ancestral adult organs are represented in the larvae. The larva in almost every case has been much reduced in size in comparison with the ancestor, which it represents. If larval organs were reduced on the same scale as the whole animal they might be reduced to dimensions which would render their functions difficult, if not impossible of performance. Too narrow gill-slits, for instance, might become useless owing to the viscosity of water in passing through small apertures. Hence arises a tendency to sacrifice number to size. Thus, the two series of gill-slits which the ancestors undoubtedly possessed, only one is developed in the larva in order that individual slits may have room to spread.

That a left-sided mouth and asymmetrical gill-slits should appear in a free swimming larva is only another example of an exceedingly widespread phenomenon, viz., the reflection of features belonging to later stages of development into earlier stages of ontogeny. This phenomenon is termed *Heterochrony* by Lankester.

Phylogeny. *Amphioxus* was first described and discovered by Pallas (1778), who regarded it a kind of slug (mollusc) and named it *Limax lanceolatus*. An Italian naturalist, Costa (1834) was the first to identify it correctly as a low vertebrate and called it *Branchiostoma lanceolatum*. A couple of years later Yarrel rediscovered it and gave the most popular name *Amphioxus*, a name that has come to be nearly universal, although the law of priority claims the use of the name *Branchiostoma*. Yarrel included it with fishes in the order Marsipobranchii, but any animal without gills, heart, brain, endoskeleton and paired eyes and other sense organs cannot be grouped under Pisces. Besides these characters, *Amphioxus* possesses colourless blood and its pharynx is surrounded by the atrium. Therefore a new group Cephalochordata was established for *Amphioxus* and the same has been raised to the status of a subphylum now.

From the study of morphology and anatomy of *Amphioxus* it is evident that it possesses practically the full complement of chordate characters and differs from the craniates in the relative simplicity of its bodily organisation. The opinions, however, are divided on its position. Some regard it as primitive whereas, others consider it to be modified or degenerate.

The primitive features which *Amphioxus* seems to share with the prechordate ancestor include (i) the naked notochord from end to end; (ii) the complete myotomic segmentation from end to end; (iii) the absence of jaws for biting; (iv) the absence of paired fins; (v) simple one-layered epidermis; (vi) the simple straight tubular intestine with a very simple liver diverticulum and the ciliary method of feeding (without its extreme specialization); (vii) the simple circulatory system without a specialized heart; (viii) segmental nephridia, which are not coelomoduct; (ix) segmental gonads with no ducts, (x) the separate dorsal and ventral roots of spinal nerves, (xi) small almost yolkless egg, hollow spherical blastula, embolic gastrulation and formation of anterior coelomic pouches.

Amphioxus also possesses certain characters which are supposed to be specialized features. The peculiar pharynx, for instance, is the most important of such characters. It has very large number of gill-slits, which have increased far beyond the number of metameres that carry them and have probably multiplied by secondary polyisomerism. Most ciliary feeders rely on their peculiar pharynx for the maintenance of a current of water from which the food is sifted. The collection of sufficient amount of food particles is possible when large amount of water passes. Increase in the number of gill-slits makes this possible. The food sifting is made possible by the presence of the elaborate velum and oral hood equipment. Besides these, the atrium and atriopore and the distortions of the coelom associated with the atrial system, constitute other such specialized features.

The degenerate characters of the brain include: (i) the reduced brain and sense organs probably in response to the assumption of sedentary life, (ii) the extension of the notochord up to the anteriormost tip of the body.

Amphioxus has been regarded as a generalized chordate. This has been very clearly expressed by the statement, "That if *Amphioxus* had not been discovered it would have to have been invented." Its structure throws much light on the form of ancestral

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chordate, but unfortunately gives no hint of the way in which it might have evolved from any known type of non-chordate animal.

Recent studies, however, link them with the tunicates. It has already been pointed out that there exists a similarity in the mode of development in the nervous system in ascidian tadpole and the *Amphioxus* larva. The notochord appears similarly in both and presents similar structure. The pharynx with its complicated equipment including the endostyle, epipharyngeal groove (dorsal lamina), etc., is similar in both. Atrium and atriopore in the larval forms are similar. The natural conclusion is that the two groups (the Tunicata and Cephalochordata) show impressive correspondence in their structure and embryonic development and, evidently enough, possess common ancestry.

CLASSIFICATION

The subphylum Cephalochordata has only one class.

Class: Leptocardii. Slender fish-like Chordata in which epidermis is one-layered, many gill-slits occur and there are no scales.

(*Branchiostoma*, *Amphioxus*).

Part Two
TYPES OF VERTEBRATES

2. Class Cyclostomata

The Cyclostomata are vermiform Craniata with smooth, scaleless skin and suction mouth devoid of jaws. The tongue is piston-like with horny epidermal teeth. They attach themselves to the side of fishes or other objects by their round mouth, (cyclo round + stoma, mouth) and may even cut a hole by file-like horny teeth that cover the muscular tongue. Thus, they are committed to a life of parasitism that may even result in the death of the unfortunate host. Many of the customary fish-like structures are lacking in cyclostomes. These include paired fins, scales, swim-bladder, cloaca, oviduct, true mesodermal teeth, vertebral centra, ribs, etc. They have only one external nasal opening, and breathe by means of 6-14 pairs of internal gills in lateral sac-like pouches. Heart is two-chambered, with auricle and ventricle (without conus arteriosus). Two kidneys with ducts to urinogenital papilla occur. Brain is differentiated and with ten or eight pairs of cranial nerves and each auditory organ with one or two semicircular canals. The skeleton consists of the notochord and various collections of cartilage. The notochord remains well developed throughout life as an axial stiffening rod and is enclosed in a thick fibrous sheath continuous with a layer of connective tissue which also encloses the spinal cord. Into this sheath are laid certain cartilaginous thickenings (arcualia) comparable with vertebrae. In the tail region these pieces fuse to form a continuous plate. The gonad is single large without duct. Fertilization is external and development is direct in some (hagfishes, slime eels) and with long larval stage (lampreys) in others. Cyclostomes are usually marine in habitat although they frequent freshwater to breed. Some species are permanent inhabitants of fresh water. Hagfishes are found up to the depth of more than 300 fathoms. The Cyclostomata are of special interest as they present characteristics possessed by early vertebrates.

TYPE LAMPREY

The lamprey-eels are far from the true eels that belong to the class Osteichthyes.

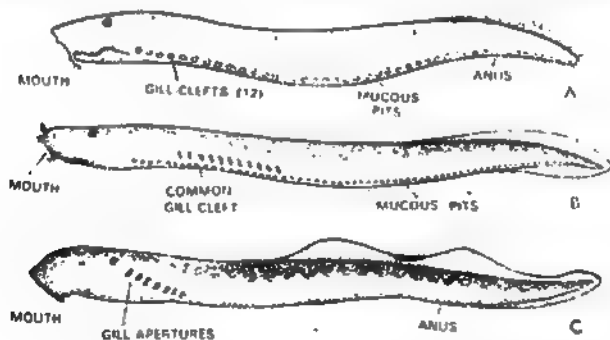


Fig. 2.1. Important cyclostome genera: *Bdellostomum* (A); *Myxine* (B) and *Petromyzon* (C).

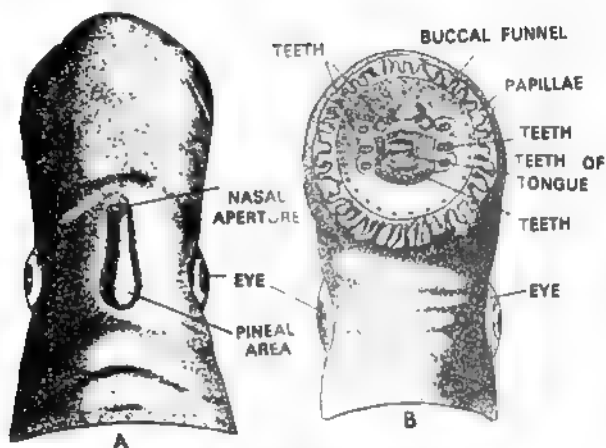


Fig. 2.2. Head of *Petromyzon*. A, dorsal view; B, ventral view

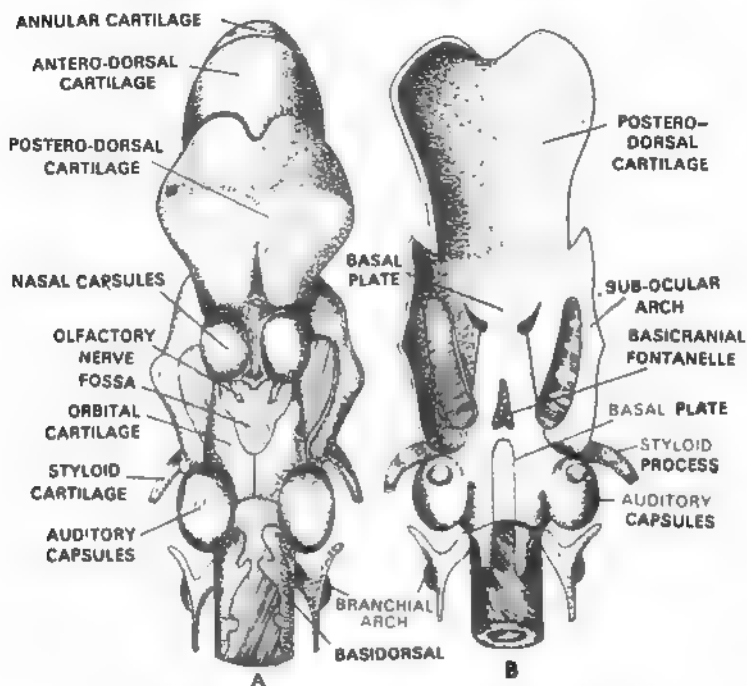


Fig. 2.3. Skull of *Petromyzon*. A, dorsal view; B, ventral view

There are numerous species of fresh-water lampreys that are generally smaller than the marine lamprey, *Petromyzon marinus*, some of the freshwater forms are nonparasitic. The marine lamprey *Petromyzon marinus* is a parasitic species and feeds during adult life preying upon fishes. The eggs of these animals hatch into larvae referred to as ammocoetes. The larval life takes between 3 to 7 years depending upon the species. The ammocoetes larva itself is harmless, but is important from the stand-point of comparative anatomy, for it presents the primitive features of a generalised chordate.

External Features. The lampreys are the most familiar among the cyclostomes and occur in temperate zone of both hemispheres. The elongated cylindrical body possesses a laterally compressed tail. Paired fins are not present, but the tail bears a median fin which extends anteriorly as dorsal fin. The female possesses a distinct anal fin. The dorsal fin of mature specimens also shows sex-difference in shape. The head of

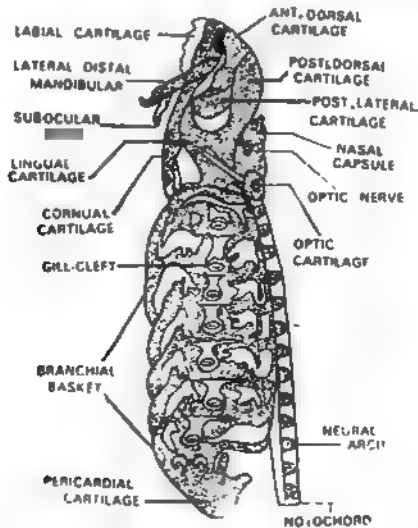


Fig. 2.4. Lateral view of the skull and branchial basket of *Petromyzon marinus* (after Kingsley).

lamprey bears a pair of laterally placed eyes covered by transparent skin. On the dorsal side there is a single nasal opening, and behind this there is a gap in the pigmentation of the skin through which the third pineal eye is visible as yellow spot. Ventrally, on the head there is large cup-like buccal funnel (also called sucker), margined by soft papillae and lined within by conical yellow horny teeth. There are seven pairs of gill-openings beginning behind the eyes and extending posteriorly. Along each side of the body and tail occurs a row of segmentally disposed small lateral sense pits. The anal opening is ventral at the base of the tail. Close behind the anus lies a small urinogenital papilla pierced by a duct.

Integument. The surface is smooth with no scales and the skin is many layered very different from that of *Amphioxus*. The epidermis is the outermost layer, followed by cutis, subcutis and finally the musculature. The inner layers of epidermis are protoplasmic and become progressively cornified as they pass outwards. Cornification takes place as a result of the production of a compound called keratin. Such a protective layer occurs in all vertebrates. Many gland cells occur in the epidermis as in other aquatic vertebrates. These produce slime. The cutis is a layer of bundles of collagen and elastin fibres, running mostly in a circular direction. Below this lies a

distinctly marked-off layer, the subcutis, consisting of connective tissue, fat and blood vessels. Star-shaped pigment cells occur in the cutis and also form a thick pigment layer at the junction of cutis and subcutis. The pigment in these cells possesses the ability to migrate, making the animal pale or dark. In the larval lamprey this change is especially well marked.

Muscular System. The segmental musculature of cyclostomes presents the same generalized plan as in *Amphioxus*. Regular segmental myotomes or myomeres run uniformly from head to tail with no regional specializations except where they are interrupted by gill-slits and eyes. Between adjacent myotomes are myocommata, tough connective tissue partitions. On the back of the head each myotome is W-shaped instead of V-shaped as in *Amphioxus*. No horizontal septum divides the myotome into dorsal and ventral halves, as in true fishes because the lateral-line is absent. The muscular system of the "tongue" is a rather intricate system of muscle-bands that need not be described in detail.

Movement. The movement of lamprey is mechanically inefficient; they show great activity but move slowly. They swim rather in an eel-like manner using myotome serially. The waves pass down the body. Often it comes to rest, attaches itself to its prey or stone by suckers (hence called "suck-stone"). In this position the water enters through the gill-openings. When swimming the backward jet of water may assist in locomotion.

Skeleton. The skeleton of lamprey includes (i) the notochord with cartilaginous arcualia dorsal to the notochord, two pairs to most body segments, (ii) the complex skull; (iii) the elaborate paired visceral arches or branchial basket, and (iv) the stout lingual cartilage of the tongue, and a ring of annular cartilage surrounding the buccal funnel.

The notochord remains well developed throughout life. It is a slender gelatinous rod made up of large vacuolated cells enclosed in a thick fibrous sheath. The rigidity of the rod depends upon the turgor of the cells. The notochordal sheath is continuous with a layer of connective tissue which also surrounds the spinal cord. The cartilaginous thickenings, above the notochord, can be compared with vertebrae as similar elements in higher vertebrates from neural arches. The skull consists of a series of incomplete boxes of cartilage (Fig. 2.3) surrounding the brain and organs of special sense. To this is attached the skeleton that supports the sucker and gills. The skeleton of the branchial region consists of a system of vertical plates between the gill-openings, joined by horizontal bars above and below. This whole structure lies in the body wall, hence the question of comparison with the similar structure in the higher vertebrates does not arise.

Digestive System. The mouth is at the centre of the buccal funnel or sucker. It is closed or opened by the forward or backward movement of the piston-like tongue. On the edges of the sucker occur a series of lips which are sensory, and make a tight attachment when the lamprey sucks. The mouth is surrounded by horny epidermal teeth, the arrangement of which varies in different types of lamprey. A section of a tooth will reveal that each is supported by a cartilage pad. The sharper and larger teeth occur on the movable tongue that is used as a rasp. The mouth leads into a large buccal cavity (also called pharynx by some). At the hinder end it divides into a dorsal food passage, the oesophagus and a ventral respiratory tube. The entrance of the respiratory tube is guarded by a velum bearing a series of velar tentacles presumably sensory (as in *Amphioxus*). The oesophagus opens directly into the straight intestine as there is no true stomach in lamprey. The surface of the intestine is increased by a typhlosole running in a spiral fashion. The intestine ends at the small anus.

A pair of pigmented sacs are embedded in the hypobranchial muscles. These are 'salivary' glands, each of which has a folded wall and gives out a duct that opens below the tongue. The secretion of these prevents coagulation of the blood of the fish on which the lamprey feeds. Exact nature of the secretion is unknown. The structures are of special interest, as salivary glands do not occur in other vertebrates, below mammals. The liver is usually without a bile duct; and the occurrence of a pancreas is uncertain. It has been observed that in lampreys taken from other fishes the intestine is

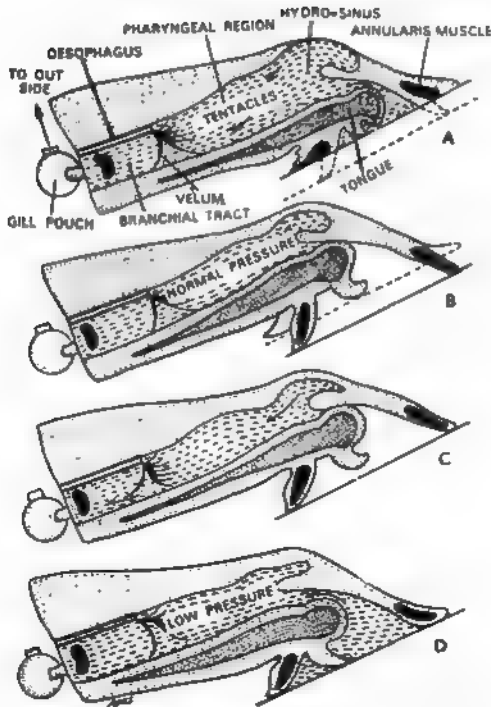


Fig. 2.5. Action of the buccal funnel and tongue during feeding and attaching in lamprey.

filled with red corpuscles and there is, therefore, no doubt that they feed mainly on the blood of their prey. Nothing much is known about their feeding habits in the sea.

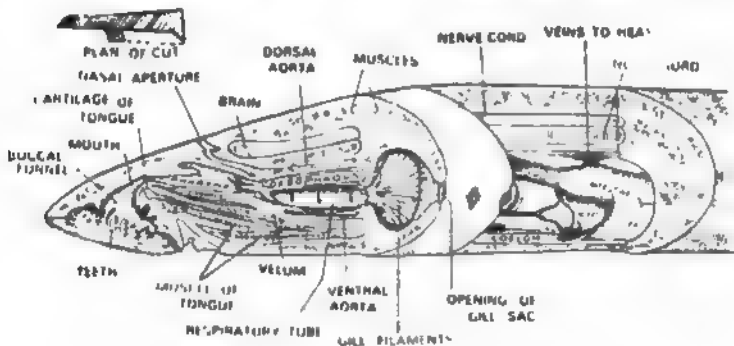


Fig. 2.6. Structure of the adult lamprey shown in sagittal section.

Circulatory System. The circulatory system of the lamprey is of the same type as that of *Amphioxus*, but a definite heart has developed. This lies behind the gills within the cup-shaped posterior end of the branchial basket and is suspended in a special pericardial sac that communicates with the coelom. It is considered to be a portion of the subintestinal vessel folded into a S-shape and divided into three chambers, the posteriormost is thin-walled **sinus venosus**, which opens into a thin-walled **auricle** or **atrium** lying above it (sinus). The auricle passes into a thick-walled chamber, the **ventricle**, below. Contractions proceed from behind forwards. The sinus venosus receives blood from veins and conducts it to the auricle. The thick-walled ventricle pumps it round the body. The blood leaves the heart by the **ventral aorta**, running forwards and giving off a series of eight pairs of **afferent branchial arteries** to the gills where aeration takes place and then it is collected in a median **dorsal aorta** that carries blood to all the parts of the body through a series of segmental arteries and special vessels to the gut, gonads and excretory organs. Curiously enough most of the major blood vessels are provided with valves at their beginning. The venous system presents simple vertebrate plan. A single **caudal vein** collecting blood from the tail divides into two **posterior cardinals** on entering the abdomen. These receive blood from the kidneys and gonads, etc., and open into the heart by a single **ductus Cuvieri** on the

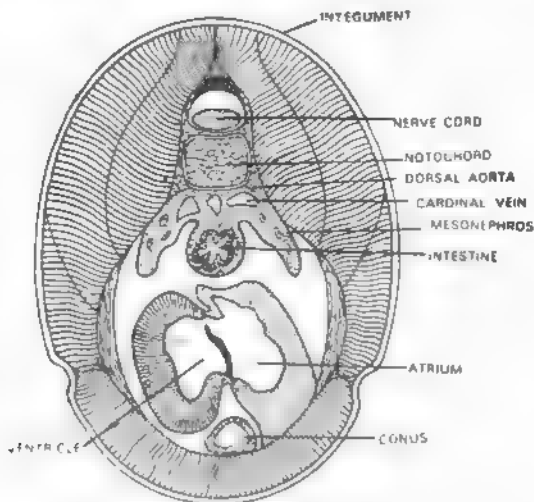


Fig. 2.7. Cross-section of ammocoetes larva showing chambers of the heart.

right hand side (in the embryo both are present). **Anterior cardinals** collect blood from anterior side of the body. A **hepatic portal vein** collecting blood from the alimentary canal is present. There is no renal portal system. Lymphatic vessels are also present. The blood contains the respiratory pigment within nucleated corpuscles, white corpuscles also occur. It is not known how the blood corpuscles are produced. The spleen is absent, therefore, it is believed that the corpuscles are produced in lymphoid tissue in the kidneys and elsewhere.

Respiratory System. There are seven pairs of obliquely placed gill-pouches between the respiratory tube and the body wall. Each gill-pouch contains many gill-filaments with fine capillaries in which aeration actually takes place. Water enters the gill-

pouches through the same opening through which it comes out. It is not so in fishes. The reason for this peculiarity is that the lamprey attaches to its prey or other objects by its buccal funnel (Fig. 2.8), as such water cannot enter through the mouth. In the larval stages the normal course exists, that is, water enters through the mouth and comes out of the gill-openings as in fishes.

Nervous System. The nervous system shows an advance over that of *Amphioxus* and presents vertebrate plan. As a result of high degree of cephalization the front end of the spinal cord is enlarged into a complicated brain and the nerves connected with that portion have become cranial nerves. The forebrain includes large paired **olfactory lobes**. The **cerebral hemispheres** are small attached to the **diencephalon**. Beneath the latter lies a broad **infundibulum** and the **pineal** or **median eye** dorsally. This is the so-called **third eye** better developed in these animals than in other living vertebrates. The structure of these shows that they are eyes with little special differentiation. The midbrain has a pair of large optic lobes rather dorsally placed. The hindbrain is differentiated into a small transverse dorsal band, the **cerebellum**, and a much larger ventral **medulla oblongata**. Between the optic lobes and the medulla extends the **choroid plexus** containing rich blood supply. The **spaces or ventricles** within the brain are four as in other vertebrates. The cranial nerves are 10 pairs.

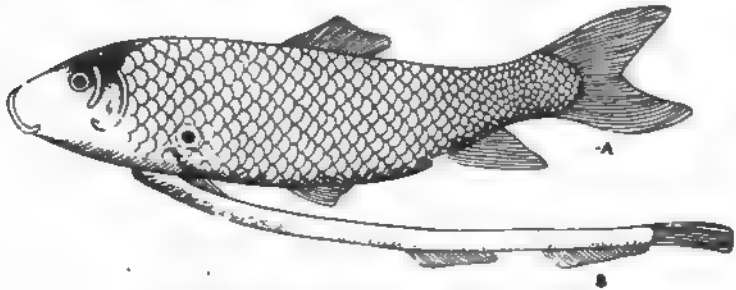


Fig. 2.8. Diagram shows a lamprey (B) attached to a fish. (A).

The **spinal cord** is dorso-ventrally flattened and band-like structure of uniform transparent grey colour. The spinal nerves are like those of *Amphioxus* in that the dorsal and ventral roots do not join. In *Amphioxus* the dorsal roots contain sensory fibres and motor-fibres for the lateral plate musculature, while the ventral roots contain only motor fibres. In the case of the lamprey the details of the composition of the nerves are not known, but it is believed that considerable deviations have occurred from this plan. The sympathetic nervous system is poorly defined.

Sense Organs. The single nasal aperture leads into an **olfactory sac** innervated by nerve endings from both the olfactory lobes of the brain. The paired eyes present the same structure as is found in a normal vertebrate eye. The eyes are formed as a result of evaginations of the wall of the diencephalon, the optic nerve, therefore, is not a nerve but a portion of the brain. For this reason some authors choose to call it optic tract. There are six extrinsic muscles controlling the movement of each eye. They are arranged unusually and probably have different types of innervation. The power of accommodation does not lie in the iris, outlining a round pupil, which shows practically no change under different illuminations. On the other hand, there is a **cornealis muscle** pulling on the cornea. A contraction of this muscle flattens the cornea and pushes the lens behind. What is the use of these eyes to the animal is not known. In the larva the eyes are buried under the pigmented skin. It is not certain that the prey is searched with the help of the eye or smell.

The **pineal** or **epiphysial eye** presents an elaborate eye-like structure with a clear lens and pigmented retina. On the basis of recent evidence it can be said that the pineal eye has nothing to do with the initiation of movement or the perception of light. In the

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ammocoetes larva there is a daily rhythm of change of colour—the animals become dark in the daytime and pale at night. If the pineal eye is removed the colour remains continually dark. The change of colour is brought about by the action of nerve impulses from the pineal eye. "It seems that the pineal apparatus is an organ concerned with adjustment of internal activities of the animal to correspond to the changing condition of illumination."

The lateral-line sense organs are peculiar to fish-like vertebrates. They occur in the lamprey on the sides of the body and the under surface of the body. Each is a little patch of sensory cells innervated by fibres from cranial nerves, those on the trunk and the tail getting fibres from a special branch of the vagus nerve.

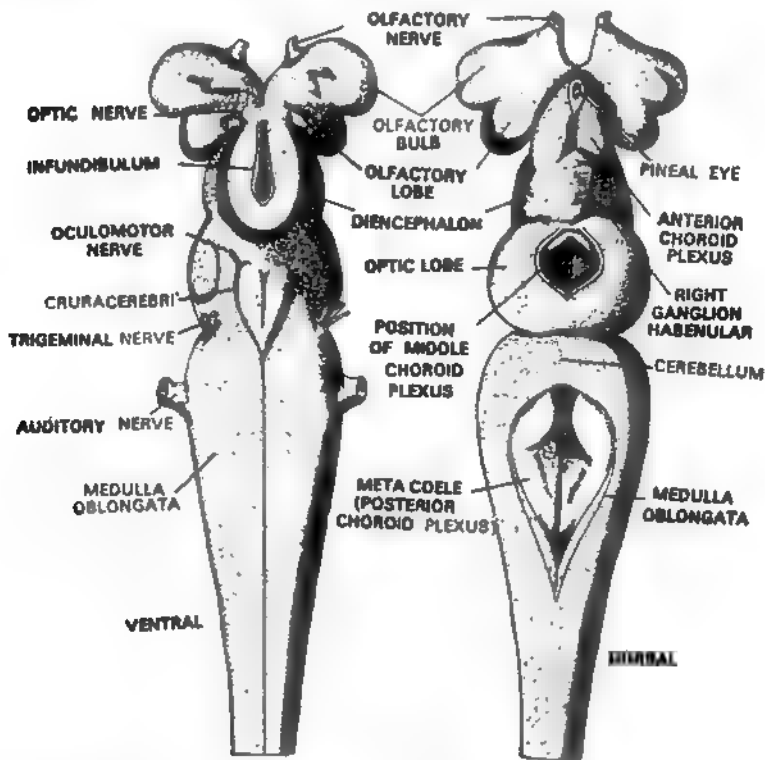


Fig. 2.9. Brain of *Petromyzon*. A, dorsal view; B, ventral view (after Parker and Haswell).

The auditory sacs are formed as a result of the inpushing of the wall of the head which ultimately becomes cut off from the exterior. As a result of complications the sac is divided into several chambers. The sacculus and utricle are two pockets to which are connected two tubes, the semicircular canals, set at right angle to each other. They are organs that help the animal to maintain equilibrium.

Taste-buds occur in the pharynx; and there are light sensitive cells (photoreceptors) in the skin as well as in the eyes. They are numerous in tail and if the tail is exposed to light the animal moves away quickly.

Endocrine glands. The pituitary body lies beneath the infundibulum. The major portion of the pituitary gland is a mass of secreting cells in which two parts can be recognized, **anterior and intermediate**. If the pituitary is removed the animal remains pale in colour. This secretion presumably is under the control of the pineal eye. The functions of pituitary are similar to those of other vertebrates.

The pituitary is associated with a long posteriorly directed sac extending from the olfactory sac. This is the **naso-hypophyseal sac**. In all vertebrates the pituitary develops as a ventral pocket from the floor of the brain and another dorsal pocket from buccal ectoderm. In all vertebrates the latter loses its connection with the buccal cavity, but in the adult lamprey the sac becomes enlarged extraordinarily and opens with the nostril on the dorsal surface of the head. Thus a connection between the nose and the pharynx is established. During respiratory movements the nasohypophyseal sac is squeezed and water is expelled from the nostril with force. When the gills relax water gets in and the olfactory organ is provided with the samples. If the nasohypophyseal opening is plugged the lamprey does not react to solutions such as alcohol which normally it tries to avoid.

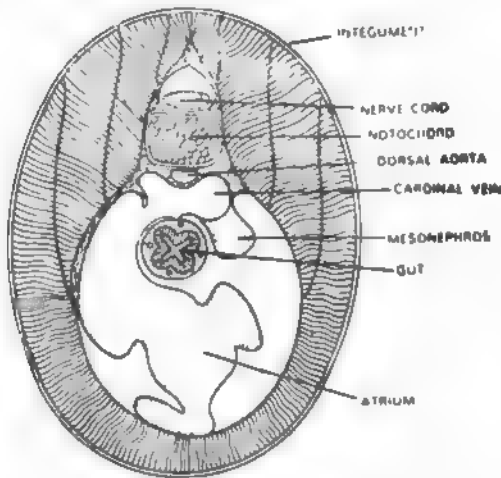


Fig. 2.10. Cross-section of ammocoete showing the formation of mesonephros.

Urinogenital System. The urinary system includes two **kidneys (mesonephros)** which lie dorsally in the body cavity. From each arises a tubular **ureter** and runs to the **urinogenital sinus** which opens to the exterior on the **urinogenital papilla**. The gonads develop from ridges of tissue lying medial to the mesonephros on each side. The differentiation of the gonad takes place quite late in life, as such in the young lamprey the organ contains developing oocytes and spermatocytes together, i.e., it is **hermaphroditic**. But later on the gonad becomes either **testis** or **ovary** or that the sexes in the adults are separate (dioecious) although hermaphroditic specimens are occasionally encountered. The ripe ovary consists of ova, each surrounded by a single **layered follicle**. The testis consists of a number of follicles containing **sperms**. The gonads have no ducts. Ova or sperms are released in the coelom by the rupture of the gonads. The sex cells escape through **genital pores** developed just before mating. These pores are similar in the two sexes and consist of short channels, one on each side, leading from the coelom to the lower end of the kidney duct. Normally they open a few weeks before spawning. Fertilization is external, but the cloaca is differently modified in two sexes to ensure

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fertilization and proper placing of the eggs. In mature male the lips of the cloaca unite to form a narrow tube-like penis. In the female the cloacal lips are enlarged and often red. The female also possesses the anal fin which probably helps in making a nest (as in salmon and trout).

Petromyzon marinus leaves the sea and goes to fresh water streams to spawn. Such animals are called **anadromous**. Not being a strong swimmer it makes its way to the spawning ground with some difficulty. For this purpose it moves by making short spurts, fastening its suctorial funnel to a stone or other object, resting a bit, and then repeating the process. A small area or nest, 6 to 24 inches in diameter, is hollowed out in the gravel and rubble in the river or stream bed. This is accomplished by fastening its funnel to a stone and then wriggling backwards. Such a process is repeated several times. The eggs are laid in this nest. A single female may lay 100,000 eggs. Soon after

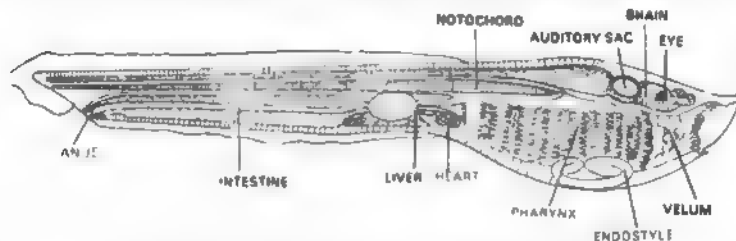


Fig. 2.11. Longitudinal section of ammocoete larva showing its general structure.

spawning the adult animals die and their bodies disintegrate rapidly as the animal is without much skeletal material. The eggs are yolk-y but the cleavage is total as found in the case of the frog. After about two to three weeks the young hatches as the **ammocoete** larva about 10 m.m. in size. This tiny creature is transparent. But it grows up into an opaque eel-like creature about 170 m.m. long. The larval life is relatively long from three perhaps to seven years. They live in burrows in the sand for three years or more before undergoing metamorphosis. The young lampreys then migrate downstream and out to sea.

Ammocoete larva. On hatching the small larva swims for a little while and soon burrows in the soft mud of the river bottom and banks. When undisturbed the larvae are fully buried in mud. Food is drawn in by the water current produced by the rhythmic movement of the gills, and appears to be drawn mainly from adjacent mud surface where detritus and small organisms are settling. The buried larvae emerge

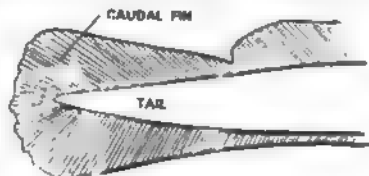


Fig. 2.12. Caudal fin of ammocoete.

occasionally to change their feeding ground as and when they find the mud less nutritious. There is no sucker, the mouth is lodged in a small depression and is surrounded by an oral hood (as in *Amphioxus*). The developing lateral eyes become covered with opaque skin and the larvae are blind. The pineal eye remains light sensitive but is concerned less with any form of vision than with diurnal change in pigmentation of the skin from dark by day to pale by night. Active light response comes from photoreceptors in the tail, which inform a burrowing ammocoete whether its rear end is within the mud or still sticking out of it.

The particles of food enter the pharynx with water. Before they pass out of the gill-slits they are caught by a column of flowing mucous cord into the mid pharynx, produced by a comparatively short but complex endostyle. The mucous food cord rotates in the current and passes directly back to the oesophagus. The feeding mechanism of this type is found in larvacean and thaliacean tunicates. No enzymes have been discovered in the endostyle, its main function is to produce mucous. It is not an open groove like the *Amphioxus* but presents similar arrangement of the secretory columns. In *Amphioxus* the current is set in by ciliary action hereby muscular action. This use of muscles to move the gills is regarded as an important step in chordate evolution. The ciliary method imposes limitation of size from which the ammocoete escapes. The endostyle, on the other hand, shows the survival of the primitive feeding method. On metamorphosis the endostyle develops into a thyroid gland. Nothing is known about the function of thyroid in the adult lamprey, it, however, presents the conversion of an externally secreting feeding organ into a gland of internal secretion.

As the endostyle changes into thyroid, the mouth becomes rounded, teeth, tongue and complex musculature appear. The paired eyes come up, the olfactory organs

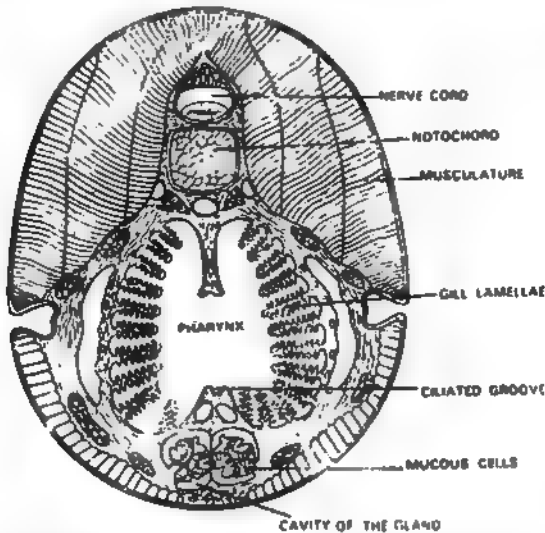


Fig. 2.13. Cross-section of ammocoete through the pharyngeal region.

mature. The hypophysial sac enlarges and extends back to the gills. The gills develop into sacs opening into the branchial chambers. Intestine becomes modified, yellow brown colour of the larva becomes dark. It frequently leaves the mud and finally migrates to the sea as adult and begins its parasitic life.

Lampreys are the lowest of living vertebrates. Both externally and internally they are rather primitive and peculiar. They are far above the lancelet stage as in addition to the notochord there are other skeletal parts of cartilage; a brain case, a highly developed set of gill-bars of peculiar construction and the beginning of a backbone. The brain with the organs of special sense is well developed. The internal ear has two semicircular canals. These peculiar animals are thus highly specialized in many ways, but are definitely more primitive than any typical fish in two important features—the absence of jaws and the absence of paired limbs. They certainly present a very low stage in vertebrate evolution but obviously they are not vertebrate ancestors.

Ostracoderms. The ostracoderms present the first opportunity of the study of fossil record. In the second period of Palaeozoic era, the Ordovician, the first faint traces of the oldest known vertebrates are available. It is in the shape of small flakes of bone in rock deposits apparently formed in shallow waters, that suggest that probably the oldest vertebrates were the inhabitants of fresh-water. These oldest fragments dating perhaps 450,000,000 years back in the earth's history are not preserved well and as such give no idea of the nature and forms of the animals to which they belong. From the fresh water deposits of Silurian and Devonian some fossils have been dug out. These include cephalaspids, pteraspids and anaspids the oldest fossil vertebrate known (except the Ordovician fragments). These animals show several characters that link them with the cyclostomes. Though rare several specimens may be found together as if they were from a single dried-up pool. In the cephalaspids the body was encased in a bony shield, whose under surface bears an imprint of the brain, nerves and branchial apparatus. The rest of the body was fish-like, with an upturned tail, and covered with heavy bony scales. A pair of flaps behind the gills probably represent pectoral fins. Pelvic fins are not traceable. Like lamprey Cephalaspids have a single nasal opening on the top of the head. Behind the nostril there is the median (pineal) eye between the paired eyes. On the underside the mouth is small, which appears to have sucked in nutritive material which was strained out in its passage to the round gill-openings at the side of the throat. In the lamprey the mouth has developed into a large sucker in response to carnivorous habits.

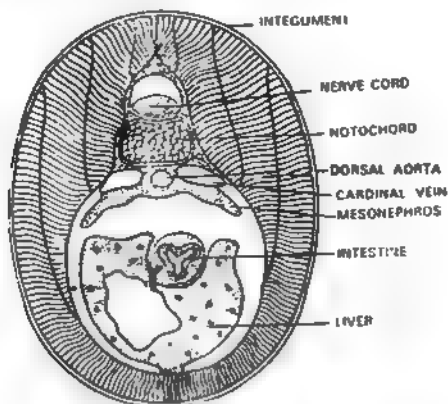


Fig. 2.14. Cross-section of ammocoete through the region of the liver

It seems likely that the jawless and limbless condition is one to be expected in the oldest vertebrates. Ostracoderms and lampreys present most primitive stage in vertebrate evolution, but it cannot be said, that ostracoderms were ancestors of lampreys. "Recent work, however, has tended strongly to show that some of the ostracoderms probably are exceedingly close to the line of descent of both cyclostomes and higher fishes. Bone, in the shape of both surface armour and internal skeletal parts, seems to be an extremely old vertebrate character. It is probable that many vertebrates now lacking such structures are degenerate rather than primitive. We know, for example, that such a fish as sturgeon, with hardly a bone in its body, has descended from forms with a well-ossified skeleton, and it is highly probable that other modern forms which have no bones, such as lampreys and sharks, are in reality degenerate rather than primitive types. Armour was probably a character common to all ancestors of vertebrates and the ostracoderms are really an ancestral group" (Romer). These jawless

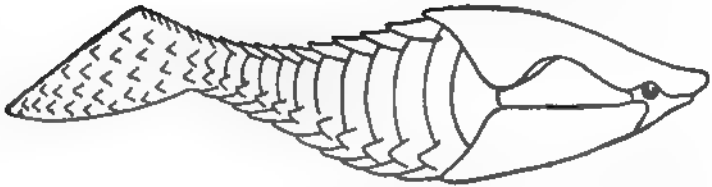


Fig. 2.15. Ostracoderm.

animals led the life of grubbers in the mud. With development of the jaws in some unknown form, the predatory life began. The development of the jaws thus made the next great advance in vertebrate evolution.

CLASSIFICATION

The class Cyclostomata are naked eel-shaped vertebrates with no jaws or paired fins and with a single median nostril. The group is divided into two orders, the Petromyzontia and Myxinoidea.

Order 1. Petromyzontia. Lampreys. The Cyclostomata in which the mouth is surrounded by a large ventral suctional funnel bearing many horny teeth. There is a dorsal nasal sac not connected to mouth. The eyes are present. There are seven pairs of gill-pouches opening separately (Fig. 2.1). Eggs are small, but the larval stage is long. Occur along sea-coasts and in streams and lakes, all over the world *Petromyzon marinus* is a well-known example, other examples include *Entosphenus tridentatus* (Pacific lamprey), *Ichthyomyzone concolor* (silvery lamprey).

Order 2. Myxinoidea. Slime Eels or Hagfishes. The Cyclostomata in which the mouth is nearly terminal and four pairs of tentacles are present around the margin of the mouth. The nasal sac is near the end of the head and is connected to the pharynx by duct. The eyes lie beneath the skin. There are ten to fourteen gill-slits that open into a common chamber before opening by a single Branchial basket and arcualia are poorly developed. The eggs are large and develop directly. These marine animals eat their way into the flesh of fishes *Myxine glutinosa* is the well-known example. Other species include *Myxine limosa* (Atlantic coast), *Bdellostoma* (Chile), *Petistorema* the "borer"

3. The Chondrichthyes

Appearance of the Jaw. The next evolutionary step is the appearance of well-jawed predators from the jawless mud-grubbers. The ostracoderms and lampreys present jawless forms. But in another group called **Placodermi**, now extinct, the oral arch is more or less differentiated to form jaws. The jaws of these ancient fishes were in the experimental stage, and were sometimes only poorly developed sometimes quite aberrant in nature. The fishes bearing them were armoured without exception. Most characteristic of these fishes were the spiny sharks (Acanthodians). These were still river dwellers and were still well armoured, covered with scales and plates of bone-like material. A peculiar side branch of these primitive forms is that of 'jointed-necked' fishes (Arthrodires) of the Devonian, *Dinichthys*, the best example of this group was a giant form (about 26 feet long) with massive jaw-like structures which are thought to have operated in a peculiar fashion. From such beginnings have appeared the modern sharks with true jaws. Once the shark reached sea the abundant food supply forced them to turn into powerful predators. Along with the development of jaws and teeth the vertebrates left the bottom and became predacious type, preying on larger things. This mode of life required faster locomotion, therefore, the body became streamlined and paired locomotory fins also developed.

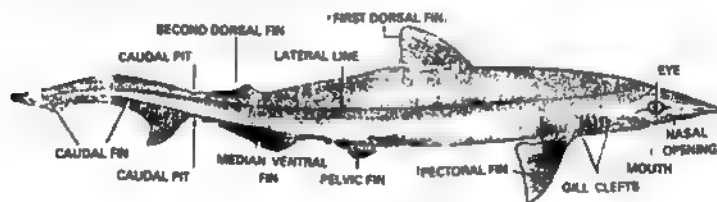


Fig. 3.1. Lateral view of *Scoliodon* showing the external features.

The **Chondrichthyes** (Gr. *chondra*, cartilage + *ichthyes*, fish) is a class of vertebrates containing cartilaginous fish. In these animals true bone is absent although deposition of calcium takes place in the cartilage. The copulatory organs are complicated formed from the pelvic fins of males and are called claspers. These are almost exclusively marine and unlike the other fish classes, have been so throughout their known history, though ancestors were probably fresh-water forms. They appeared first in the Devonian some 300 million years ago. The class includes the Selachii (sharks, dogfish, skates and rays) all bearing placoid scales, Holocephali (chimaeras) and some fossil groups. These fishes, it is apparent, vary from graceful, streamlined specimens such as sharks to much-flattened rays and skates. The cartilaginous fishes are very numerous at present, but were far more numerous in ancient times as is confirmed by their fossil history.

The elasmobranch (literally 'plate-gilled') fishes occur in all parts of the sea. They include sharks ranging from monsters of thirty feet long to the common dogfish, *Scoliodon sorrakowah*, 12 feet. Nearly all elasmobranch fishes are carnivorous or

scavengers. They also have bottom feeding members, the skates and rays, feeding mostly on invertebrates. The sharks are quite numerous, well suited to marine life and have active predacious habits that enable to feed upon more elaborately built bony fishes. The characteristic feature of the dogfish is that its entire internal skeleton is made up of cartilage (hence Chondrichthyes). This was formerly regarded as a primitive feature. But it is not so. Bone is quite old in evolutionary history. The absence of bone, therefore, is a secondary feature. They have given up their defensive armour because of the development of other means of protection. These include swift running, good sense organs and brain, and powerful jaws.

Several varieties of sharks are found off our coasts. The description here presented is of one of the abundant species of the Indian seas, *Scoliodon torrakowah*. It is an inhabitant of the open sea and for the capture of its prey and protection it depends on swift movement. The body is perfectly streamlined, without being rigid. Projections or sharp angles are perfectly adapted for clearing the water.

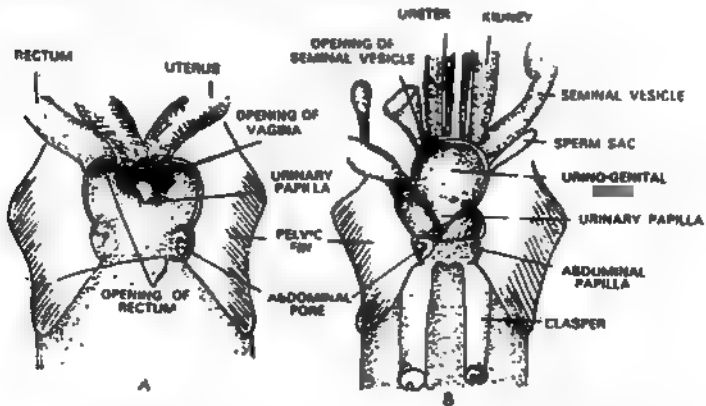


Fig. 3.2. The structure of the cloacal chamber in the female (A) and male (B) dogfish.

EXTERNAL CHARACTERS

Shape of the Body. The long laterally compressed body, tapering at both the ends, is the broadest in the region of the pectoral fins. The dorso-ventrally compressed head is produced into a flat pointed snout anteriorly. The head bears two large circular eyes at its sides, the eyelids are immovable and can hardly be distinguished from the surrounding integument, but each eye is provided with a special eyelid, the nictitating membrane, which lies along the anteroventral border and can be drawn over the eye in time of danger. The pupil is narrow and vertical. The trunk passes on into tail compressed from side to side and slightly bent upwards. At the junction of the trunk and tail there are two shallow pits—one dorsally and the other ventrally. These are the caudal pits. A mere touch reveals that the entire body is covered with minute scales. A careful look reveals the presence of a faint line, the lateral line, extending from the head to the posterior end of the body.

The body supports several fins that help the animal in locomotion and in maintaining balance. The fins are flattened expansions of the skin, usually triangular in shape and supported by cartilaginous rods and horny fin-rays. Among the median fins the first dorsal fin is large triangular in shape situated a little in front of the middle of the body, the second dorsal fin is situated a little distance behind the first and is similar in shape though smaller in size. The caudal fin forms a vertical fringe round the posterior portion of the tail. It is divided into two lobes—dorsal and ventral. The dorsal lobe

forms a low ridge along the greater part of the upper surface of the tail in the median line. The ventral lobe is well developed divided into two parts, a larger anterior and a smaller posterior. The ventral median fin (anal fin, Fig. 3.1) is situated in the mid-ventral line slightly in front of the caudal fin. This is almost opposite to the second dorsal fin. Comparable with the limbs of higher vertebrates there are two sets of paired fins. Originating from the ventro-lateral margins of the body immediately behind the gill-clefts are the pectoral fins, triangular in shape and ending over a long space. These are the largest among fins. The pelvic fins are smaller in size and similar in shape. They arise close together from the ventral surface of the body a little in front of the middle of its length. Their inner borders touch each others and in male are fused together behind. They enclose the cloacal chamber. In the male a part of the fin, on each side, forms a copulatory organ, the claspers. Each clasper is a stiff rod-like appendage grooved dorsally. The groove leads into a cavity, the siphon, beginning at the base of the clasper.

External Apertures. Situated on the ventral side of the snout is a wide crescentic opening, the mouth. It is bounded by the upper and lower jaws, each bearing one or two rows of oblique teeth. On the ventral surface of the body between the pelvic fins there is an elongated opening, the cloacal aperture (Fig. 3.2). The nostrils are a pair of obliquely placed crescentic apertures on the under surface of the head in front of the mouth. A small fold of skin from the anterior edge covers each nostril partially. The

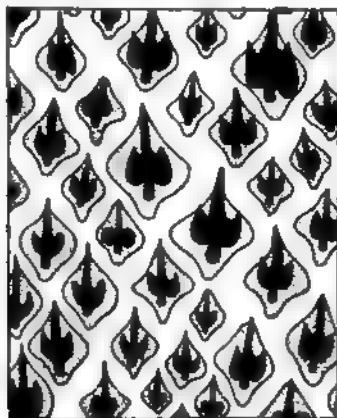


Fig. 3.3. The placoid scales on the surface of the skin.

nostrils are only olfactory, as such, they do not open internally into the mouth cavity. For breathing there are a series of five vertical slits, the gill-clefts, on each side, in front of and slightly above the pectoral fins. The gill-clefts open obliquely backwards into the gill-pouches and the pharynx. The abdominal pores are a pair of openings situated on elevated papillae, the cloacal papillae, on either side of the cloaca. Through these minute pores the coelom communicates with the exterior. What is the exact function of these abdominal pores is not known. On careful examination the head shows numerous groups of small openings on the sides and on the snout. These are the apertures of the ampullary canals. If the head is squeezed minute droplets will be observed pouring out of the openings.

Exoskeleton. The skin is covered with minute dermal denticles or placoid scales which are arranged in regular oblique row and form the exoskeleton of the shark. These scales are derived from the skin. Each scale (Fig. 3.4) consists of a diamond-shaped calcified basal plate from which a flat trident spine projects out. The spines are

directed backwards. The basal plate is formed of calcified tissue closely allied to the cement of our teeth. A small opening in the centre of the plate leads into a cavity, the **pulp cavity**, which traverses the spine and is filled with pulp containing numerous dentine forming odontoblast cells. The spine is made up of **dentine** (Fig. 3.4), a calcareous substance externally covered by another hard dense **enamel-like material**. The dentine is relatively spongy through which ramify numerous fine branches or **canaliculi**.

The form of the spine differs in different parts of the body. On the ventral surface the spine has one point and on the dorsal three points. The scales in the skin which covers the lips bounding the mouth, and which is continued in the buccal cavity over the jaws, are larger and stronger. They have a trilobed base and a five-pointed spine and function as teeth. Really speaking the structure of these dermal denticles and the teeth

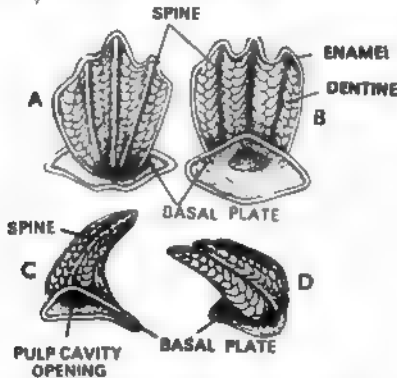


Fig. 3.4. Structure of the placoid scale. A, dorsal view; B, ventral view; C, ventrolateral, and D, dorso-lateral.

of higher vertebrates presents striking similarity in structure.

The scales are being constantly worn away and equally constantly replaced, so that in a vertical section of the skin they appear in various stages of development. Normally the scales are set closely together in the skin. The enamel-covered spines are so strong that the dried skin of some dogfish and sharks, known as **shagreen**, is used for making the surface smooth.

Development of Placoid Scales. The first indication of the developing scales is the accumulation of mesenchyme cells in the dermis to form a **dermal papilla**. As this increases in size it projects upwards into the dermis, pushing the Malpighian layer outwards. The cells of the outer margin of the dermal papilla form a layer of **odontoblast** cells which secrete a hard bone-like substance, resembling dentine of the teeth of higher vertebrates. This substance is closely related to bone. The cells of the basal epidermal layer, overlying the dentine-like substance, then form an enamel organ composed of columnar **ameloblast** cells which produce a hard, enamel-like coating over the outer portion of the conical mass of dentine (Fig. 3.5). As this tooth-like structure or scale grows in size it pushes the epidermis aside and emerges above the surface as a placoid scale.

The **cosmoid scale** consists of three¹ layers. The outer layer, formed of a cell-less substance somewhat like dentine, is called **cosmine**. It contains vascular spaces and fine radiating canaliculi. On its outer surface the cosmine contains a thin layer of hard glossy substance the **vitrodentine**. The middle layer is the vascular **bony layer** with numerous anastomosing canals for blood vessels. The innermost layer is the **isopedine** layer comprising several laminae of bone lying parallel to one another, traversed by

¹ Four according to some who classify *cosmine* and *vitrodentine* as two separate layers.

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vascular channels. During growth the cosmoid scales expand by the addition of cosmine round the edge of the upper surface and by the addition of isopodine below. They are not shed.

The ganoid scales are composed of bone and are often covered with a shiny substance called **ganoin**. They never bear enamel and are purely of dermal origin formed by the activity of the mesenchyme cells of the dermis and correspond to the basal plates of placoid scales. Each ganoid scale consists of four layers, (i) outer layer of cell-less dentine-like substance **ganoin** arranged in successive lamellae; (ii) the next is a

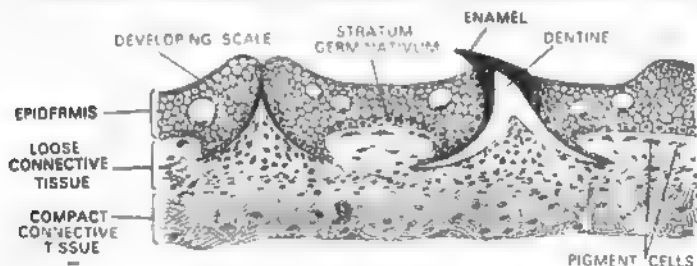


Fig. 3.5. Development of placoid scales.

cosmine-like layer traversed by canaliculi; (iii) a **vascular layer**, and (iv) the innermost layer of **isopodine**. These are not universally present. They are, however, well represented in the *Palaeoniscoid* type of the ganoid scale but in the *Lepidosteoid* type there are only three layers, outer ganoin layer, middle vascular layer rather thinner and innermost layer of isopodine.

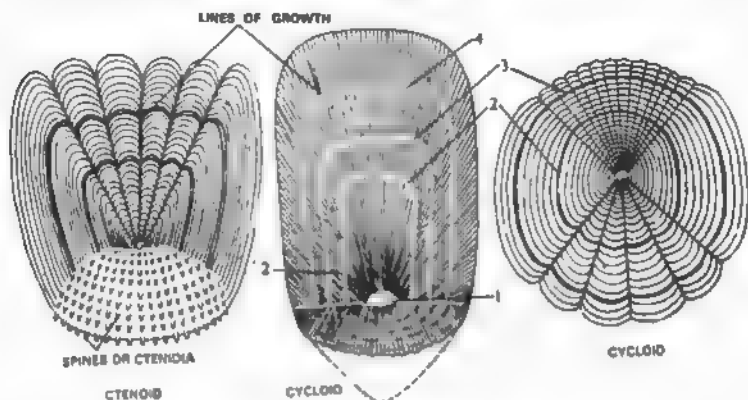


Fig. 3.6. Cycloid and ctenoid scales. 1, edge of smolt scale, 2, first winter zone mark; 3, spawning mark; 4, second winter zone mark.

The skin of the dogfish comprises two layers; an outer **epidermis** and an underlying **dermis**. The epidermis is a layer of cells, several cells in thickness. The outer cells may form a thin squamous layer covering the external surface. The basal layer of the epidermis is the germinative layer, the **stratum Malpighi**, and retains its germinative capacity throughout life giving origin to cells to replace worn out cells of the outer layers. In the epidermis also occur certain mucous secreting glands especially in connection with the ampullary and canal systems. The secretion of these cells produces

a slimy coating over the surface of the skin. Multicellular glands appear at the bases of the spines which develop at the anterior margins of the dorsal fins and in the epidermis overlying the claspers of the pelvic fins of the male.

The dermis is the underlying layer composed of scattered cells, intermingled with connective tissue fibres. Numerous pigment cells or *chromatophores*, containing black pigment occur beneath the Malpighian layer. The distribution of these cells differs in the different parts of the body. They are much more numerous on the dorsal surface than on the ventral, that is why the dorsal surface of the animal is darker than the ventral surface. The rest of the dermis consists of loose connective tissue followed by a more compact layer. The basal plates are also embedded in the layer.

Most sharks and some dogfishes have a spotted or wavy pattern, which serves to break up their visible outline as they move in the water. They are also able to change their colour, though only slowly, and become darker on a dark background.

Musculature. The greater part of the body-bulk consists of muscles packed together between the skin and the skeleton. The muscles are highly developed in the region of the trunk and tail and present a perfectly segmental arrangement comprising a paired series of muscle-segments called *myotomes* (*myomeres*) separated from one another by tough connective tissue partitions called *myocommata*. Each myotome presents a zig-zag appearance being sharply bent forwards and backwards four times along its course. In surface view the successive myotomes present a cone-in-cone arrangement. In transverse section the myotomes appear as several bundles of concentrically arranged muscle-lamellae placed one above the other dorso-ventrally.

At the level of the lateral line runs a white line of connective tissue. This is the outer edge of the horizontal skeletogenous septum, which divides the myotomes into dorsal *epaxial* muscles and ventral *hypaxial* muscles. On the ventral side there is a white partition the *linea alba* in the mid-ventral line. In the trunk the muscle-layer is greatly thickened dorsally on each side of the vertebral column pushing the body cavity enclosing the visceral organs ventrally. In the tail region, on the other hand, the muscles are equally developed on the all sides round the vertebral column and occupy all space between the skin and the column. The muscle fibres in each myotome run parallel to the long axis of the body. On contraction these fibres exert a pull on the *myocommata* which are inserted internally on the vertebral column and externally on the skin, and bring about the flexion of the body.

These muscles that ensheath the body are known as *parietal* muscles. They have, however, undergone modification because of the presence of appendages. The muscles responsible for the movement of fins bud off as muscle slips from the myotomes in the neighbourhood of the appendage. The *elevators* of the pectoral fin arise from the posterior side of the scapula and the vicinity, and run on the dorsal surface of the fin which they elevate (draw dorsally) and adduct towards the body. The *depressors* from the lateral side of coracoid, extend on the ventral surface of the fin which they depress (draw ventrally) and adduct. The small *adductors* arise from middle part of girdle, beneath membranous posterior wall of fifth gill-cleft and extend to the anterior border of the fin. They pull it forward and away from the body, i.e., adduct the fin.

In the region of the gill-slits and on the ventral surface of the head occur the *visceral* muscles, which serve to move the gill-arches and the jaws. There are a great many of them but here only the following may be mentioned. the *trapeziales*, the long muscle above the gill-slits and below the myotomes, the *dorsal constrictors*, between the dorsal portions of the gill-arches, and with their fibres directed obliquely forward; the *ventral constrictors* between the ventral portions of the gill-arches, and covering the ventral surface, extending forward to the mouth with fibres directed backwards, and the *adductor mandibularis*, the thick muscles at the angle of the jaws, used to close the lower jaw. The constrictors open the gill-slits by diminishing the distance between the gill-arches by their contraction. These muscles of the dogfish persist in higher vertebrates, although the gills have been lost and remain associated with structures derived from the gill-arches, namely, the jaws, the hyoid and the laryngeal cartilages.

Locomotion. The fins are not the organs of locomotion as was believed for a long time. They simply help the animal in keeping balance in water, in keeping constant course and also in changing the direction. The actual propulsive forces that move a fish

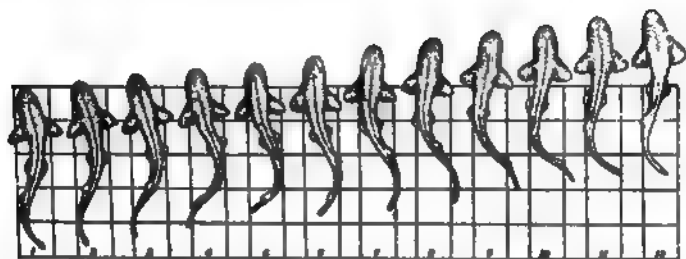


Fig. 3.7. Illustration of locomotion of the dogfish (after Gray). The photographs were taken at intervals of 0.10 second, the side of the square is three inches. The diagram shows successive positions of the dogfish in 0.10 seconds. The black dot in the figure marks the crest of a wave. The large amplitude of the movements of the body and tail is noteworthy.

through the water, are produced by the longitudinal muscle fibres of the myotomes. The myotomes comprise blocks of longitudinal muscle fibres, placed on either side of an incompressible central axis, the notochord or vertebral column. As the muscle fibres in any myotome contract, the body is bent. In forward movement the contraction of each myotome takes place after that in front of it. In this way waves of curvature pass down the body, alternately on each side. This has been illustrated by a series of photographs of the dogfish. Thus, it is evident that waves of curvature of the

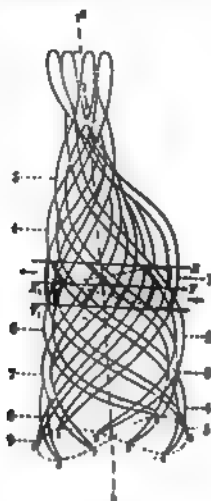


Fig. 3.8. Enlarged drawings of a young eel (*Anguilla*) illustrating the movements of short segments of the body during the passage of a complete wave past the segments (after Gray). The segment xy is travelling from right to left and is directed obliquely backwards to the left. The segment x_1y_1 is travelling from left to right and is directed obliquely backwards to the right. Note that the tip of the tail is moving in a figure of 8 curve.

body are produced by a succession of longitudinal waves of contraction on alternate sides of the fish.

The muscle contractions produce movements of the parts of the body, related to one another in such a way as to transmit a backward momentum to water. Thus, each portion of the side of the fish can be considered as moving like the blade of an oar used for sculling at the back of a boat. The essential feature is that the moving surface is inclined at an angle to its line of motion. Gray has shown this by superimposed drawings of an eel (Fig. 3.8) made from successive photographs. The region marked xy is moving from right to left and the x, y , from left to right. The following words from Gray are fully explanatory:

"All parts of the fish's body which are in transverse motion have their leading surfaces directed backward and towards the direction of transverse movement, but the angle of inclination is most pronounced when the segment is crossing the axis of longitudinal motion, and at this point the segment of the body is travelling at its maximum speed.

"There is therefore a definite angle between the surface of the fish and its path of motion." Each point of the body evidently travels along a figure of 8 curve as is indicated by dotted lines at the tail point of the eel. As a result of these quick transverse movements the inclined surface of the body pushes the water behind. Such alternate 'pushes' in quick succession give a forward thrust to the body of the fish. Evidently, the magnitude of this forward thrust depends "among other things on (a) the angle which the surface of the fish makes with its own path of motion, (b) the angle between the surface of the fish and the axis of forward movement of the whole fish, and (c) the velocity of the transverse movement of the body (Gray)". The efficiency of movement depends on the shape of the body and the action of its muscles.

Nervous mechanism also plays important part in the production of swimming waves. In the dogfish the isolated spinal cord is able to initiate rhythmic swimming. If the spinal cord is cut off from the brain the posterior portion shows swimming movement for several days. If the sides of the body are touched lightly the movements stop, they can be again initiated by some sensory impulses. All the available information on this subject is not sufficient to show how the swimming rhythm is initiated and maintained.

The fins are meant to maintain equilibrium of the body during swimming. The forces acting on a fish are measured along three main axes, longitudinal, horizontal and vertical. Deviation from the line of motion about the vertical axis is known as yawing, about the longitudinal axis is rolling and that about transverse axis is pitching. The forces along these three axes are known as drag, lateral force and lift. Recently Harris studied the function of the fins by making use of models of fishes. He established that the median dorsal fins of a dogfish act as stabilising keels and prevent rolling. They thus maintain the equilibrium in the horizontal plane. The paired and caudal fins prevent pitching, that is, maintain equilibrium in the vertical plane. "The strong lateral movements of the heterocercal tail and tail fin, during swimming, besides giving a forward thrust to the fish, produce a negative pitching reaction making the fish dive head downwards; this negative reaction is counterbalanced by a positive pitching reaction (lift force) produced by the paired fins. These fins, in fact, are essentially 'elevating planes' in the dogfish. In other words, while the movements of the tail and tail-fin tend to force the nose of the fish downwards, the "trailing" movement of the pectoral and pelvic fins tend to force the nose upwards nearly with the same amount of force. The heterocercal tail and the paired fins, therefore, neutralize each other's opposed pitching effects and thus lead to the normal equilibrium of swimming dogfish. Of the pectoral and pelvic fins it is the pectorals that largely determine the pitching stability, the contribution of the pelvic being very small" (Thilayampalam).

THE ENDOSKELETON

The endoskeleton is well developed in the dogfish, but consists entirely of cartilage, calcified at places. The primary function of the endoskeleton is to provide a system of

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rigid levers to which muscles can be attached (and does not necessarily participate in the protection of the viscera). But the evolutionary history shows that the endoskeleton may take on a protective function by developing around the heart, lungs, etc. (such as girdles and limbs). The skeleton of the dogfish may, as usual, be divided into the **axial skeleton** and **appendicular skeleton**. The axial skeleton consists, in all craniates of the skull and **vertebral column**, of which the latter is usually described first due to convenience. The appendicular skeleton consists of the **girdles** and **fins**, both **pectoral** and **pelvic**.

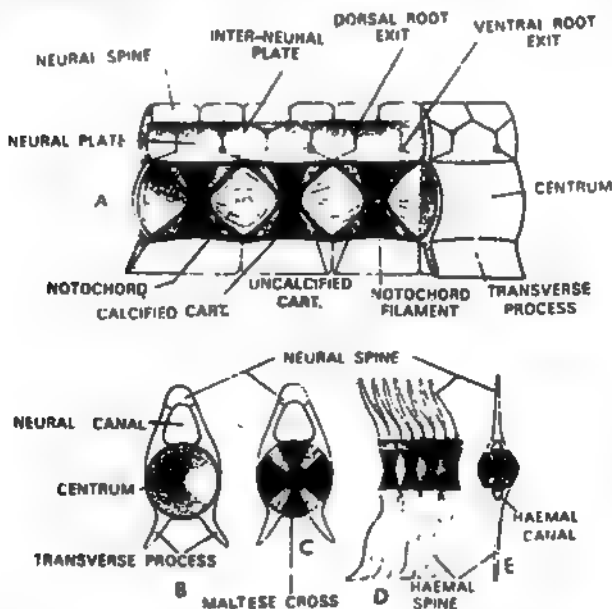


Fig. 3.9. Structure of the vertebrae of dogfish. A, a portion of the vertebral column cut partly sagittally; B, trunk vertebra, front view; C, transverse section of the same; D, longitudinal section of four tail vertebrae; E, cross-section of a tail vertebra.

AXIAL SKELETON

Vertebral Column. The vertebral column consists of a chain of cartilaginous vertebrae, but presents the appearance of intricate series of cartilaginous plates bound together by fibrous connective tissue (Fig. 3.9). The vertebrae develop around the notochord and in the dogfish they vary only slightly in shape. Taking a trunk vertebra as an example it is apparent that a typical vertebra consists of a **centrum**, around the notochord, a **dorsal neural arch** around the spinal cord, and a pair of **transverse processes** on the side, projecting ventrolaterally from the centrum. The centra are short cylindrical bodies of cartilage hollowed out at either ends, i.e., the vertebrae are **amphicoelous**. The notochord is constricted in the intervertebral space enclosed within the adjacent centra. The centra are strengthened by calcified fibro-cartilage developed as four wedges, which traverse the body of the centrum from its periphery almost to the centre thus giving rise to a cruciform figure looking like a "Maltese cross" which can be seen in a transverse section of the centrum through the middle. The **neural plates** are a series of hexagonal plates of cartilages forming the sides of neural

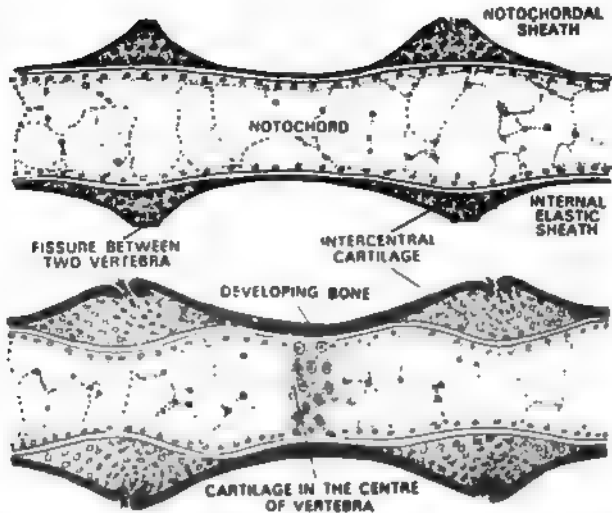


Fig. 3.10. Early and later stages of the development of a vertebra of *Amblydonna* (after Kingsley).

arches; the spaces between the consecutive vertebral neural plates, in contiguous vertebrae, are occupied by the **intervertebral neural plates** (Fig. 3.9A). The **neural arch** lies dorsal to centrum enclosing the spinal cord. Each arch is formed of elements or structures of two kinds, viz. (i) the neural processes (**neurapophyses**), the blunt bases of the neural arches projecting upward from the sides of each centrum, and (ii) the **neural spines**, a series of median nodules of cartilage completing the neural arch above. The transverse processes are a pair of blunt horizontal projections on each side of the lower surface of the centrum, in the trunk region, and bear at their anterior ends movably articulated cartilaginous ribs about half an inch in length. The **haemal arch** is found in the vertebra of the tail region. Here the transverse processes, instead of projecting laterally, are bent inwards beneath the centrum and meet and fuse in the mid-ventral line to form an arch, the haemal arch, the ribs, are therefore, absent. Each haemal arch enclosing the haemal canal is produced into a backwardly directed and flattened haemal spine, to provide support to the ventral lobe of the caudal fin. The dorsal lobe of the fin is supported by the prolongations of the neural spines. The posterior part of the vertebral column is bent up towards an asymmetrical tail that is called heterocercal tail (Fig. 3.1).

Development. The notochord is the only axial skeleton of the body in lower chordates, but it is later replaced, either in parts or completely, by cartilaginous or bony vertebrae. In all vertebrates the notochord forms the foundation around or upon which the vertebrae are formed. They are formed from the mesenchyme contributed by the **sclerotomes** of the **paraxial mesoderm**. The sclerotome is the lower part (Fig. 3.13) of the inner wall of the myotome, lying close to the notochord and since the sclerotomes arise from metameric structures they remain segmentally arranged for a time. The number of vertebrae corresponds to the number of somites in the trunk region, but a definite vertebra is not formed by the mesenchyme from the sclerotomes of a single pair of somites.

In most vertebrates the sclerotome is divided transversely into **cephalic** and **caudal** parts by a cleft (the **fi ssure of von Ebner**). The mesenchyme of the anterior part of the sclerotome, the **cranial or cephalic part sclerotome**, is less dense than that of the

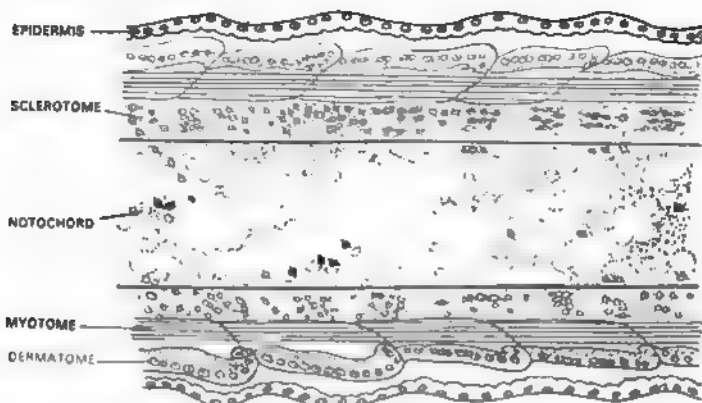


Fig. 3.11. A horizontal section of an elasmobranch embryo showing the sclerotome formation

posterior or the caudal part sclerotome. A definitive vertebra is formed by the fusion of the caudal part sclerotome of one somite with the cranial part sclerotome of the next somite caudad (towards the tail), therefore, the fissure of von Ebner marks the future articulation between contiguous vertebrae. The mesenchyme of the cranial and caudal part-sclerotomes, next, breaks away from the somites and settles around the notochord and neural tube¹, and appears as four-paired accumulations of sclerotomal mesenchyme cells in every segment below and above the notochord. These accumulations later chondrify forming distinct cartilages or arcualia. The posterior part sclerotome gives rise to a dorsal pair of arcualia, the *basidorsals* and a ventral pair, the *basiventrals*, beneath the notochord, one on each side of the dorsal aorta. Similarly the anterior part sclerotome gives rise to a dorsal pair of *interdorsals* and a

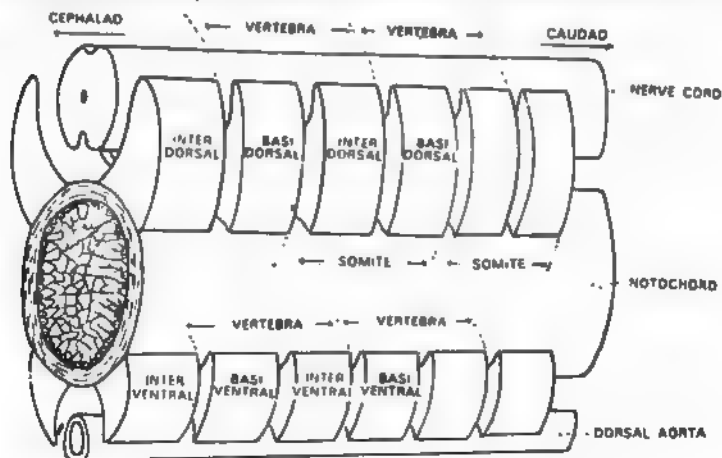


Fig. 3.12. Diagrammatic sketch showing arrangement of arcualia.

¹ In some the mesenchyme forms a continuous sheath, the *membrana reunens* around the notochord and neural tube.

ventral pair or **interventral**. Of the accumulations produced by the posterior part sclerotomes, i.e. basidorsal and basiventrals are larger and in contact with the notochordal sheath. In some, however, the interdorsal and interventrals do not touch the notochordal sheath. As the development proceeds the arcualia develop gradually enclosing the spinal cord dorsally and the blood vessels ventrally, thus, forming the neural and haemal arches. Since there are two sclerotome halves to a somite two arches to each segment may be formed. In the adult lamprey, for instance, there are two arches to each body segment, and persist throughout life though no centra are formed.

The centra are formed by the extensions of cartilage (chondrioblasts) from the bases of the neural or haemal arches, which takes place in one of the two ways: (i) The skeleton forming cells extend from the bases of the arches around the notochord (**microcentrous**) and chondrify later (Fig. 3.15). In this case the notochordal sheath remains unmodified sometimes throughout life. (ii) The cells from the bases of the arches migrate into the notochordal sheath through the *elastica externa*, and become converted into cartilage later (**chondrocentrous**).

The formation of centrum does not depend on arcualia alone. Mesenchyme also condenses internal to the arcualia forming a cylinder of **perichordal mesenchyme**

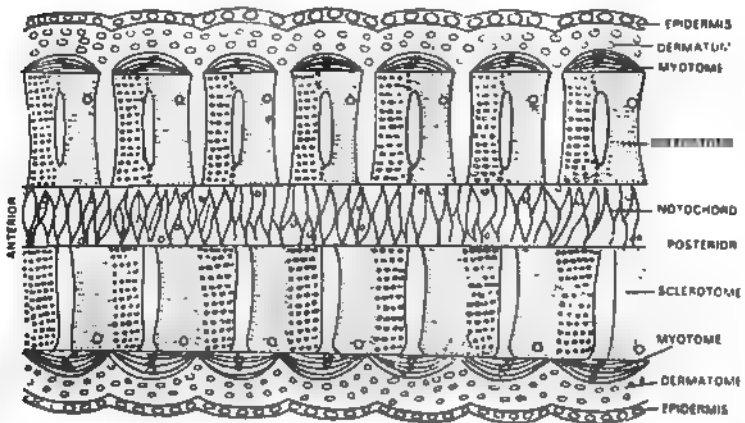


Fig. 3.13. A horizontal section of a vertebrate to show the relation between myotome and sclerotome. The upper half of the figure represents the relations in the earlier stage and the lower half represents a later stage. The posterior half of each sclerotomic unites with the anterior half of the following to form a definitive vertebra.

around the notochord. This may produce a **bony perichordal centrum**. In teleostean fishes and amphibians a perichordal centrum is formed as a rule, the arcualia playing a minor role in the formation of the centrum. Ordinarily the perichordal centrum is formed first in cartilage, but the cartilage stage is skipped in teleosts. In amniotes the perichordal mesenchyme may condense to form two embryonic cartilages, a **hypocentrum** and a **pleurocentrum** on each side and these with arcualia contribute to the formation of a vertebra.

It is evident from the foregoing that the centra are formed from elements, from two sources, they are, therefore, double in nature. In some rare cases (as in the tail of *Amia*) the double nature is evident in the adult stage. This condition has been called **diplospondyly**. The fusion of the two elements forming a definitive vertebra takes place in two ways: (i) Cranial and caudal half-sclerotomes of the same myotomic

somites unite so that the resulting centrum coincides with the myotome in position. Such vertebrae occur in some regions of a few fishes. (ii) In the majority of vertebrates the caudal half of one somite fuses with the cranial half of the succeeding somite to form a definite centrum of the adult. In this way there is brought about an alternation of myotomes (and the resulting muscles) and vertebrae, a condition more advantageous for the interaction of skeleton and muscles, because where the vertebrae and muscles are co-extensive flexure of the body to right and left cannot be affected so well.

In other vertebrates such as the Dipnoi the vertebral column continues straight up to the end of the tail dividing the tail into the symmetrical dorsal and ventral halves. Such a tail is said to be **diphycercal**. In the teleostean fishes the tail is heterocercal in enclosing the notochord. There is a prominent **occipital condyle** on either side of the earlier stages, but as the development proceeds the upper lobe shrinks and disappears and the small ventral lobe becomes large and divides into two symmetrical lobes. Such a secondarily symmetrical tail is called **homocercal tail** (Fig. 3.1).

The skull in the dogfish consists of a brain box or **cranium** with an incomplete roof, a pair of thin **olfactory capsules** (**ethmoid region**) anteriorly, a pair of stout **auditory capsules** (**auditory region**) and **occipital region** posteriorly and at the sides are the shallow **orbits**. Because the cartilaginous condition is retained in the adult, it is called a

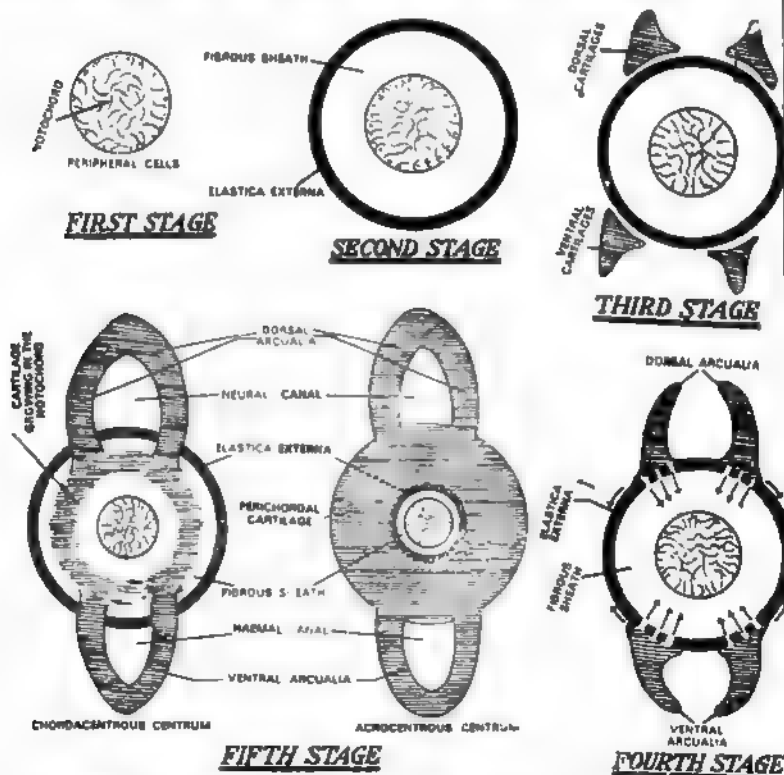


Fig. 3.14. Different stages in the formation of centra. Two methods of the formation of centrum have also been illustrated (after Snodgrass).

chondrocranium. The brain-box or cranium (Fig. 3.16) is a simple cartilaginous cylinder open in front and behind. The roof is arched and the floor flat. Anteriorly it gives off three cartilages which are prolonged forward to form the rostrum. The **occipital region** (Fig. 3.16 B) forms the posterior part of the cranium enclosing the large median opening, the **foramen magnum**, below which lies a cup-shaped concavity

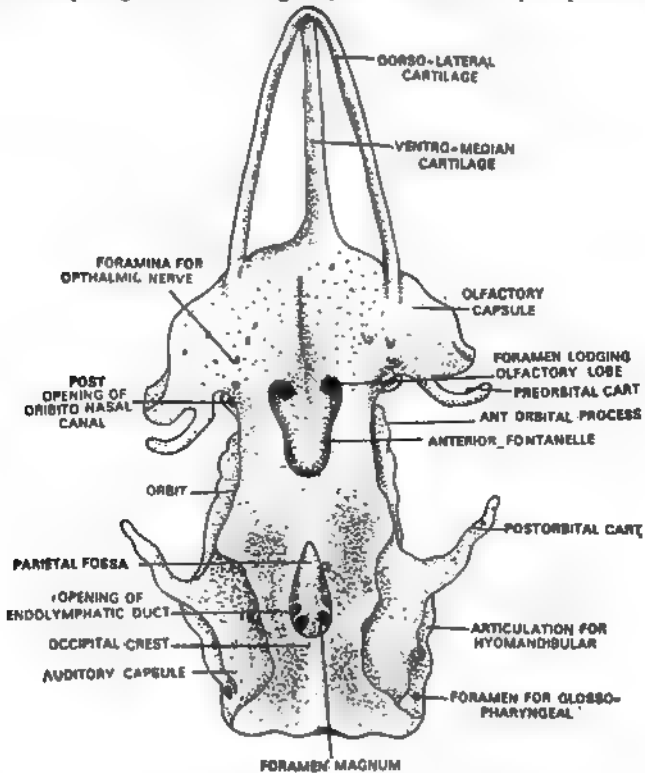


Fig. 3.15. Dorsal view of the skull of *Scalloodon*

foramen magnum. These articulate with the first vertebra. Above the foramen on the roof of occipital region there is a prominent median ridge, the **occipital crest**. External to the occipital condyles, on either side, lies a large foramen for the exit of the tenth nerve, the **vagus**. The **auditory region** consists of the **auditory capsules** and the part of the cranium they are fused with. The large laterally projected auditory capsules lodge the auditory organs, as such, the outer surface shows three prominent ridges lodging the three semicircular canals of the ear, which can usually be seen through the cartilage. Of these the anterior vertical semicircular ridge is a low ridge on the anterior side. The posterior vertical ridge lies on the posterior side, and external or horizontal semicircular ridge is on the ventral side.

Development of the Skull. In the early embryo the brain and sense organs are enveloped by a membrane of connective tissue (membranocranium of some authors), which provides the substance in which the cartilaginous skull is formed. At this stage the notochord reaches just behind the hypophysis and beneath the mid-brain. The

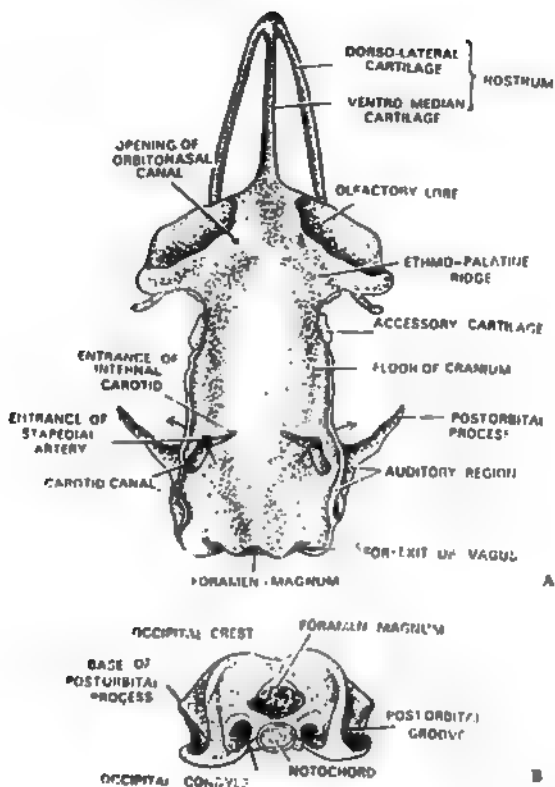


Fig. 3.16. A, ventral view of the skull, and B, posterior view of the occipital region of the skull of *Scollodon*.

three pairs of sense organs, the olfactory pits, eyes and ears, are arranged along the side of the brain and are without any skeletal support (Fig. 3.18)

Soon two pairs of flat independent cartilages appear beneath the anterior part of the brain. They support the brain from underneath. Jaw muscles may also be attached to them. Of these the anteriorly placed pair is known as the *trabeculae* or *prechordalia*, while the pair of cartilages placed under the posterior part of the brain, or either side of the tip of the notochord is known as the *parachordalia*. The sense organs also acquire, by this time, the protection of the delicate cartilaginous sensory capsules, the olfactory, optic and otic capsules associated respectively with the nasal pits, eyes and internal ears.

The three pairs of sense capsules are independent of the four primitive cartilaginous floor boards, which themselves are entirely independent. But the cartilages grow rapidly and eventually fuse forming a single continuous plate, which encloses the tip of the notochord at its posterior end, and joins with the olfactory and auditory capsules, the optic remaining free as they (the eye-ball capsules) have to rotate freely. The auditory capsules are entirely surrounded and embedded in the skeletal cartilages except for the passage way for the auditory nerve. The capsules of the olfactory pits

Hence this stage has been referred to as "underpinning" stage by some authors.

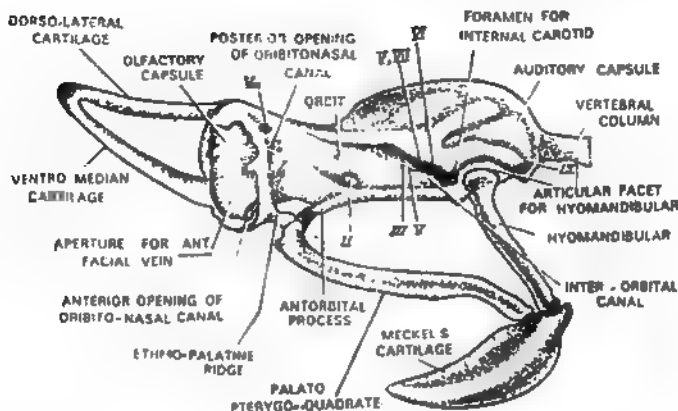


Fig. 3.17. Lateral view of the skull of *Scollodon*.

fuse solidly on their posterior and inner surfaces with the cartilaginous skull. From behind they are perforated by olfactory nerve.

In the cartilaginous platform, thus formed, there is an opening, the **hypophyseal fenestra**², around the developing pituitary body. The part of the plate formed by the parachordals, beneath the posterior part of the brain and in between the auditory capsules is called the **basilar plate**. Anteriorly it fuses with the caudal parts of the prechordal cartilage. The prechordal bars fuse with each other at their anterior ends to form the **ethmoid plate** beneath the olfactory lobe of the brain. Anteriorly it is drawn

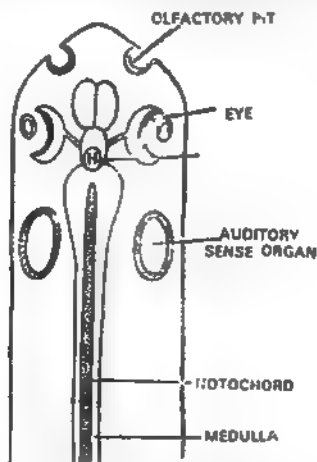


Fig. 3.18. Head of a developing vertebrate before the appearance of cartilages.

² If the fenestra **hypophyses** is large as in elasmobranchs and amphibians, etc. the skull is called **platybasic** (Fig. 3.20); if it is small, trabeculae meet just in front of the fenestra, the skull is **tropbasic**.

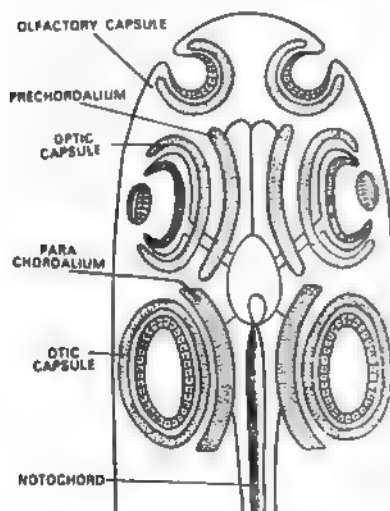


Fig. 3.19. The cartilages appear, prechordalia parachordalia and the sense capsules.

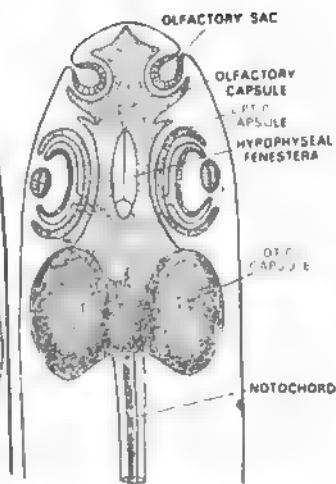


Fig. 3.20. All the cartilages fuse to form chondrocranium or primordial skull.

out laterally forming the *cornua trabeculae*, ventral to the nasal organ. Behind the ethmoid plate the prechordal bars of the opposite sides are not allowed to meet, by the developing pituitary body, leaving an opening, the *hypophyseal fenestra*, which in some closes gradually by the extension of cartilage from the sides forming a pocket, the *sella turcica*.

The platform, thus formed, serves for support and protection. The protective function is soon extended to include the sides of the brain by the upward growth of the edges of the platform in between the sense capsules. This makes the cartilaginous skull look like a trough lodging the brain. Soon a cartilage extends forward from the anterior surface of the auditory capsules, on either side forming a somewhat similar trough for the anterior part of the brain. This is the *alisphenoid cartilage* (or *ala temporalis*). The raised edges of the trabeculae forming the sides in this region, ventral to the alisphenoid cartilages have been called *trabeculae cranii*.

In the more primitive vertebrates the growth at the margins of the developing cartilaginous skull continues until the edges meet above and fuse forming the roof or the *tegmen cranii*. The *tegmen cranii* is usually incomplete, having one or more gaps or *fontanelles*, closed by membrane. The skull of the dogfish is a continuous cartilagi-

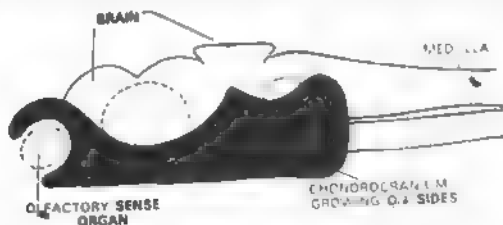


Fig. 3.21. Lateral view of the developing chondrocranium showing the formation of the sides.

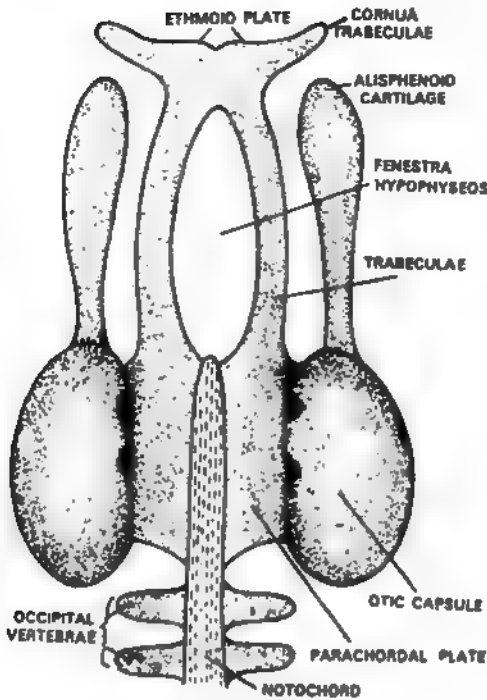


Fig. 3.22. Early (pluteus) chondrocranium of an elasmobranch straightened out (after Kingsley).

nous casket formed in this way. It has no sutures to demark its separate components and has fontanelles in the roof (see later). In higher vertebrates the cartilaginous roof is not formed fully. At the most it is represented by a mere arch, the *synotic tectum*, between auditory capsules of two sides.

The *nasal capsules* developed around the olfactory organs are fenestrated and become united to the cornua, alisphenoids and ethmoid plate. The optic capsules form the *sclera* (or sclerotic coat) of the eye. Behind the auditory capsules and around the notochord a varying number of occipital vertebrae are formed. In sharks and most teleosts they are four, in others three and in amphibia two. Like the vertebrae of vertebral column they also alternate with myotomes and nerves. Later on, however, they fuse with the rest of the cranium.

The cartilaginous envelope of the brain so formed is known as the *chondrocranium*, which is practically complete in the elasmobranch fishes and persists throughout life. In the sturgeon, *Acipenser*, the cartilaginous skull is overlaid by certain definite bony elements formed in the dermis, outside the chondrocranium, hence called *dermal bones*. These bony elements ("shingles" of some authors) do not fuse together but retain their identity. The inner cartilaginous envelope overlaid by the dermal bony elements persists throughout life in this case.

On the roof of the cranium lying between the two capsules, there is a marked depression, the *parietal fossa*, with a pair of apertures on each side of its posterior part. The posterior pair are the *fenestrae* or the openings of the *perilymphatic spaces* of the two capsules whereas, the anterior are a pair of apertures through which the *endolym-*

phatic ducts (aqueductus vestibuli) of internal ear pierces the cranium. The orbit (Fig. 3 20) lodges the eye-ball and its muscles. The dorsal boundaries of the orbits are formed by the **supraorbital crests**, which are prominent curved ridges of cartilage, running along the sides of the skull from the olfactory to the auditory capsules. Further the boundaries on the other sides are marked by the **pre-orbital cartilages**, which are slender cartilages arising from the roof of each orbit, and curved backward partially encircling the orbit, and the **postorbital cartilages** on each side arise from the auditory capsule and curve forward along the upper border of the orbit. The base of the cranium gives rise to a lateral outgrowth, the **suborbital ridge**, in the orbital region. Anteriorly this ridge is produced into the **antorbital process**. A small cartilage for the insertion of the ligaments of the upper jaw is attached to this.

Foramina. The **orbito-nasal foramen** is a small circular aperture at the anterior (inferior) angle of the orbit. The **optic foramen** is large aperture for the optic nerve at about the middle of the orbit near its ventral border. The foramen for the third nerve is a small hole in the inner wall of the orbit behind and above the optic foramen. The foremen of the fourth nerve is a small hole vertically above the optic foramen often pushed a bit posteriorly. The foramen of the fifth and seventh nerves is a large hole immediately in front of the auditory capsule. The sixth nerve also enters the orbit through the same opening. The aperture of the interorbital canal is a circular opening in front of the large aperture for the fifth and seventh nerves. The **interorbital canal** traverses the base of the skull and places the orbital blood sinuses of the two sides in communication. The foramen for the spiracular epibranchial artery into the cranium lies slightly anterior to the above. The foramen of the hyoidean artery lies a little below the aperture of the interorbital canal. The foramina for the ophthalmic branches of the fifth and seventh nerves are two separate apertures near the posterior end of the orbit

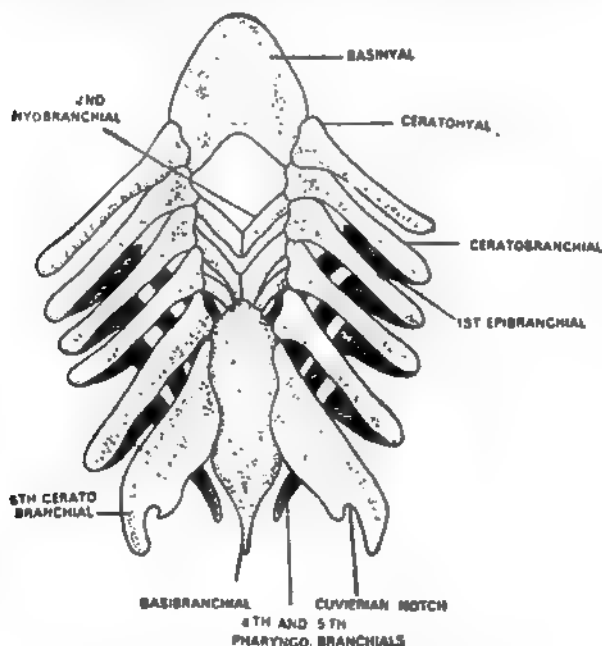


Fig. 3.23. Ventral view of the visceral skeleton of *Scoliodon*.

just in front of the auditory capsule and above the foramen for the main branches of the fifth and seventh nerves.

The **ethmoid region** consists of the olfactory capsules and the rostrum. The **olfactory capsules** are two large oval cartilaginous cups at the anterior end of the skull, firmly united to the cranium in the adult condition. A thin median cartilage, the **internasal septum** separates the two olfactory capsules from each other. The cranial roof in this region is incomplete, there being a large anterior **fontanelle** covered over by a sheet of connective tissue. Within each olfactory capsule there is a large opening leading into the cranial cavity for the entrance of the olfactory nerve. The **rostrum** is formed by three cartilaginous bars. In front of the anterior fontanelle arises a pair of **dorso-lateral cartilages** one from the roof of each olfactory capsule. These run forward to converge and meet in front with a **median ventral cartilage** which projects from the base of the cranium. The floor of cranium is broad and flat and bears towards its hinder end two obliquely transverse grooves, the **carotid canals** (Fig. 3.16). The anterior half of each carotid canal bears two apertures, one leading into the cranium and transmitting the **internal carotid artery** and the other leading into the orbit transmits the **stapedial artery**. Immediately behind the olfactory capsules lie two large and prominent articular surfaces for the attachment of the **ethmo-palatine ligaments**

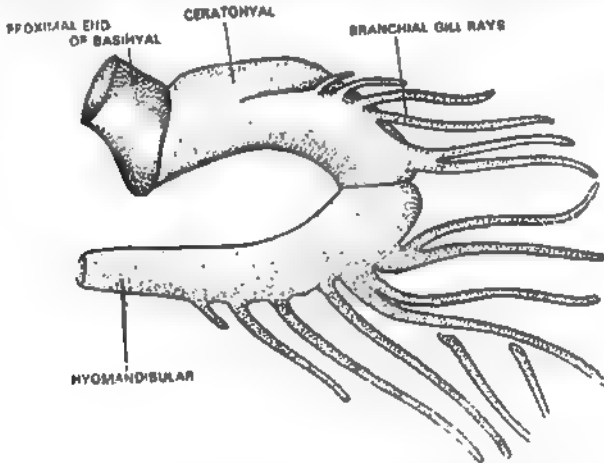


Fig. 3.24. Structure of the hyoid arch of *Scudiodon*

of the upper jaw, while in the front of these articular surfaces lie the anterior opening of the **orbito-nasal canals**. The articular surface for the **hyomandibular** cartilage is a concave depression on the side of the hinder end of the skull, below the auditory capsule.

Visceral Skeleton. The **visceral skeleton** (Fig. 3.23) is made up of a series of **visceral arches** which develop in the pharyngeal wall between the visceral clefts. Typically each visceral arch is an incomplete ring of cartilage consisting of **basal piece** in the mid-ventral line, with which articulate a series of pieces on each side extending upwards almost to the middorsal line. It is clear, therefore, that the skeletal arrangement here is independent of the chondrocranium and strictly speaking is not even a part of the axial skeleton, though for convenience it is usual to consider it to be so.

In dogfish seven visceral arches are developed, and it is the first two which warrant special attention. The **mandibular arch** is the first pair bordering the mouth and modified to form the jaws. It has lost its original arch form and consists of four pieces of cartilage, two on each side of the mouth and all joined by ligaments. Laterally on

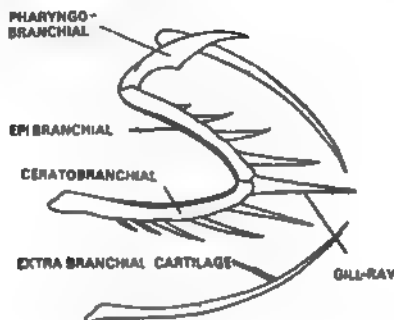


Fig. 3.25. A typical branchial arch of the dogfish.

upper jaw the **palato** or **pterygoquadrate bar**, above, and lower jaw, **Meckel's cartilage**, below, meet behind the mouth. The two rami of the upper and lower jaws meet anteriorly in the middle. The jaws have no direct connection with chondrocranium, which is provided by the second or hyoid arch. The hyoid arch (Fig. 3.16) is a loop of cartilage made up of five pieces. The **basihyal** is a median piece of cartilage lying between the rami of the lower jaw. It is rounded anteriorly and produced behind into two horns which are attached by ligaments to the dorsal surface of the **ceratohyals**. The **ceratohyals** are two cartilages each of which is long and slender and runs forwards and inwards in the floor of the mouth articulating with the basihyal at its lower end. Each carries gill-rays along its posterior border and lies in the anterior walls of the gill-clefts. The **hyomandibulars** are two cartilages dorsal to the ceratohyals. Each hyomandibular is a short stout rod fitting at its upper end into depressions in the auditory capsules of the chondrocranium to which they are attached by ligaments. These cartilages are the sole direct skeletal connections between the jaws and the cranium forming on each side, the **suspensorium** of the upper and lower jaws. Such a skull in which the hyomandibular forms the suspensorium is called **hyostylic skull**. The **branchial arches** are the remaining five visceral arches lying in relation with the branchial clefts. They gradually diminish in size antero-posteriorly. Each arch is made up of a variable number of cartilaginous pieces. In the dogfish each is divided transversely into four segments. A dorsal **pharyngobranchial**, an **epibranchial** and a **ceratobranchial** supporting the sides and a **hypo-branchial** supporting the floor of the jaw (Fig. 3.25). The labial cartilages are two pairs of slender cartilaginous rods in the folds of the skin at the sides of the mouth.

APPENDICULAR SKELETON

The appendicular skeleton includes the median fins, the paired fins and their girdles. Of the median fins there are two dorsal (anterior and posterior dorsal) and two median ventral fins. The paired fins include the pectoral and pelvic fins with their girdles.

Median Fins. The skeleton of the generalized median fin consists of a series of cartilaginous rods called **somactidia** or **pterygiophores** bearing distally a double series of horny fin-rays or **ceratotrichia**. A wide strip of ligamentous tissue connects the somactidia of the fin with the vertebral column. Each typical somactid is three segmented being made up of **proximal**, **mesial** and **distal segments**. In the case of the first dorsal fin are present twenty-one somactidia, the proximal ends of which are fused along the posterior border forming an oblique axis of the fin (Fig. 3.26). The other median fins, such as the second dorsal and median ventral, are built on the same plan. In the caudal fin somactidia are absent. The lobes of the fins are supported by elongated neural and haemal spines.

Pectoral Region. The pectoral girdle (Fig. 3.27) consists of two half loops of cartilage

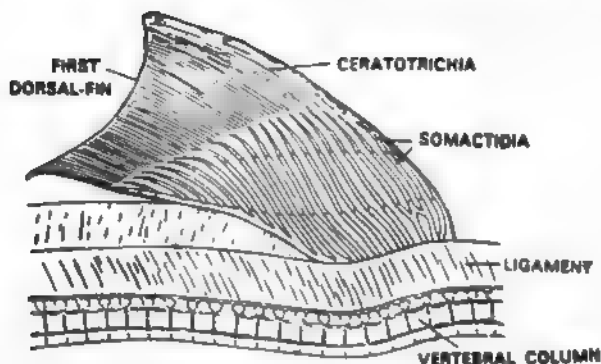


Fig. 3.26. Side view of the vertebral column carrying the first dorsal fin

fused in the mid-ventral line and free at the dorsal ends. Each half of the girdle is called a *scapulocoracoid*, the dorsal one is the tapering *scapular* region and the ventral one is the broader *coracoid* region. In the mid-ventral portion of the girdle, at the junction of two coracoids, is a well-defined depression, the *pericardial depression*, lodging the pericardium and the heart in life. The pectoral fin (Fig. 3.26) articulates, with the girdle by three basal cartilages the *pro-*, *meso-*, and *metapterygium*. Arising distally from these are the radial cartilages or the cartilaginous *fin-rays*. Each consists typically of three pieces, thus forming three rows, the second and third row are not uniform because the pieces forming these take the form of interfitting polygonal plates. The periphery of the fin is formed by an upper and lower series of horny fin-rays or *dermotrichia*.

Pelvic Region. The pelvic girdle is very simple in its structure. It consists of a simple bar of cartilages, the *ischiopubic bar* embedded transversely in the ventral body muscles, in front of the cloaca. The pelvic fins (Fig. 3.28) articulate with the ends of the pelvic girdle. Each is made up of a single basal cartilage, the *basipterygium*, supporting

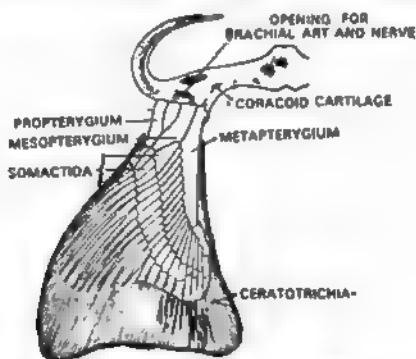


Fig. 3.27. Half of the pectoral girdle and the pectoral fin of *Scolludon*.

a fairly uniform series of *radials*. As in the pectoral fins the peripheral portions of the fins are formed of *ceratotrichia*. In the male the two pelvic fins become modified to form the copulatory organs posteriorly. In connection with each *basipterygium* there

is a grooved, backwardly directed cartilaginous prolongation which forms the axis of the **intromittent organ** or **clasper**. Each is a grooved tube open at both ends. Distally the groove ends in a sharp **style** enclosed by two covering plates, or sheathing plates of which one is dorsal and the other ventral. At the upper end of the style lies a serrated **accessory cartilage**. At the base of the clasper, in some dogfish, lies a blind muscular sac or **siphon**, which when filled with water is used to force out spermatic fluid.

Coelom and Viscera. The spacious **coelom** is divided into two unequal cavities, the **pericardial** and the **abdominal**, separated from each other by a membranous partition, the **septum transversum**. The **pericardial cavity** is a small triangular space lying beneath the pharynx and surrounding the heart. The **abdominal cavity** is quite large surrounding the viscera and communicating with the exterior through the abdominal pore. The abdominal cavity is lined with a smooth membrane, the **peritoneum**. The gut is suspended in the body cavity by a double fold of peritoneum called **mesentery**. In *Scoliodon* the mesentery is incomplete. A large flap of mesentery, **mesogaster**, suspends the stomach and another, posterior part, **mesorectum**, suspends the hinder part of the gut. The fold of mesentery suspending other organs are called **omenta** (singular omentum). The **gastrohepatic omentum** connects the liver with the stomach, and the **gastrosplenic omentum** connects the spleen with the stomach.

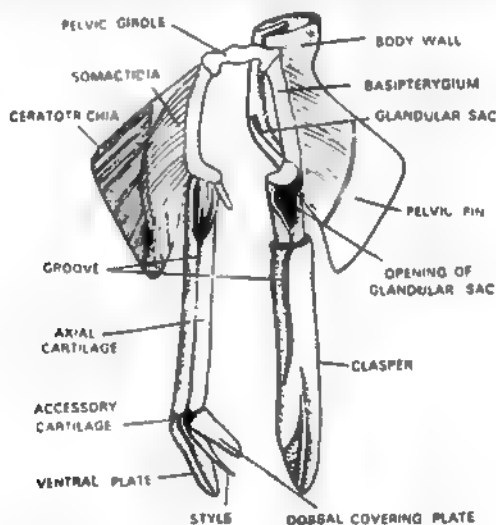


Fig. 3.28. The pelvic fin and girdle of the dogfish (dorsal view)

The **viscera** comprises the various organs lying in the body cavity, the important of which include the **heart**, almost triangular in shape lying in the pericardial cavity. The **liver** is a large compact elongated gland. It has two lobes uniting anteriorly. A median suspensory ligament connects the liver lobes with the anterior wall of the abdominal cavity. Embedded in the right lobe is found a V-shaped thin-walled sac, the **gall-bladder**. The **stomach**, a wide muscular tube, occupies the major portion of the body cavity lying between the liver lobes. Attached to the loop of the stomach is a large brownish red body, the **spleen**. The **pancreas** is a whitish, laterally compressed body, lying in the loop of the stomach and the intestine, which is a nearly straight tube running up to the cloaca.

The gonads in the female are represented by the **ovaries**, paired organs lying on the ventral side of the vertebral column just behind the base of the liver. The tubular

oviducts extend through the entire length of the body cavity uniting behind to form the **vagina** which opens into the cloaca. Between the ovary in front, and the caecal gland behind extends a long tubular strand of tissue the **epigonal organ**. In the male, however, the **testes** are a pair of elongated structures whitish in colour, lying along the dorsal region of anterior two-third of the abdominal cavity. The **kidneys** are a pair of long ribbon-like glandular structures lying dorsally to the peritoneum, and extending from the root of the liver to the cloaca.

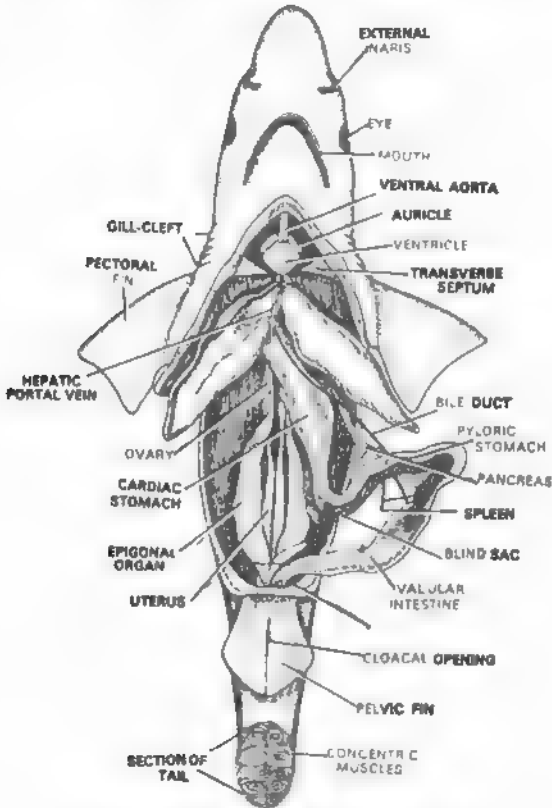


Fig. 3.29. Internal viscera of the female dogfish, ventral view.

DIGESTIVE SYSTEM

Alimentary Canal. The ventral and crescentic **mouth** opens into dorsoventrally compressed spacious **buccal cavity** which is lined with thick mucous membrane. The mucous membrane is raised ventrally into a thick fold forming the non-muscular and non-glandular "tongue." The teeth are oblique and have sharp more or less, compressed cusps, the edges of which are smooth and non-serrated. The teeth are all alike in shape, homodont, and are borne in several parallel rows (Fig. 3.30 B) on the

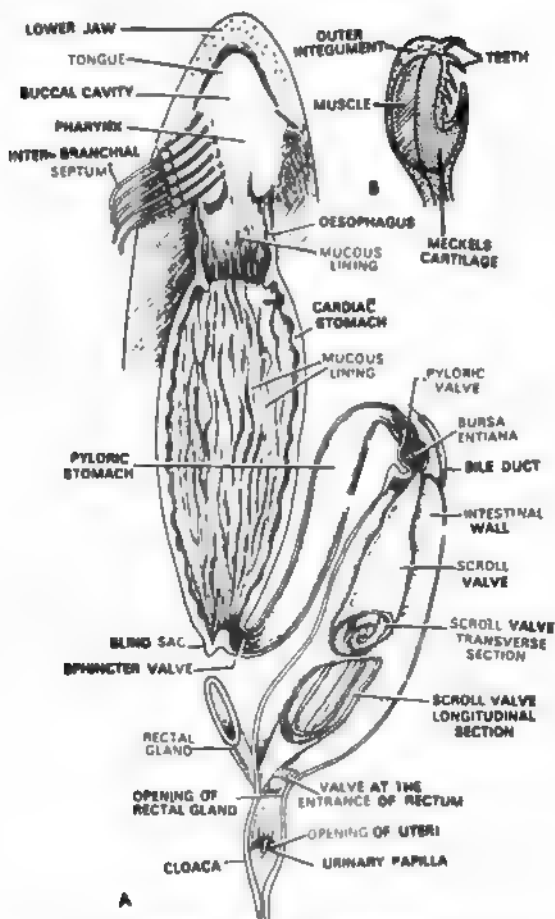


Fig. 3.38. A, alimentary canal of the dogfish partly cut open to show inner structure; B, cross-section through the lower jaw.

inner margin of the upper and lower jaws. The teeth are meant to prevent the escape of the prey rather than to bite. The buccal cavity opens into the pharynx on either side of which lie the internal openings of the spiracle and the gill-pouches. The spiracle is vestigial (not visible externally, in *Squalodon* represented by an inconspicuous oval pit). The gill-pouches are large. Internally the pharynx is lined with mucous membrane containing numerous dermal denticles. The stomach is a horse-shoe-shaped tube, the long proximal limb of which is called the cardiac stomach, whereas, the short distal limb is the pyloric stomach. At the junction of the limbs is a blind growth, the "blind sac". The inner mucous lining of the stomach is also thrown into longitudinal folds that end in the depression of the "blind sac". The lining of pylorus is quite smooth proximally but slightly folded distally. The bursa entiana is a thick-walled muscular

chamber into which the pylorus opens anteriorly. The opening of the pylorus is guarded by a pyloric valve. The bursa entiana continues into the intestine. The intestine is a wide tube running straight backwards into the abdominal cavity and opening posteriorly into the rectum. The internal surface of the intestine is increased by a characteristic fold of mucous membrane, the scroll valve, having one edge attached to the inner wall of the intestine and the other rolled up longitudinally on itself into a scroll, making an anticlockwise spiral of about two and a half turns (Figs. 3.30 & 3.32). The rectum is the last part of the gut. The caecal or rectal gland opens into it dorsally. The cloaca is the chamber into which the rectum as well as the urinogenital ducts open.

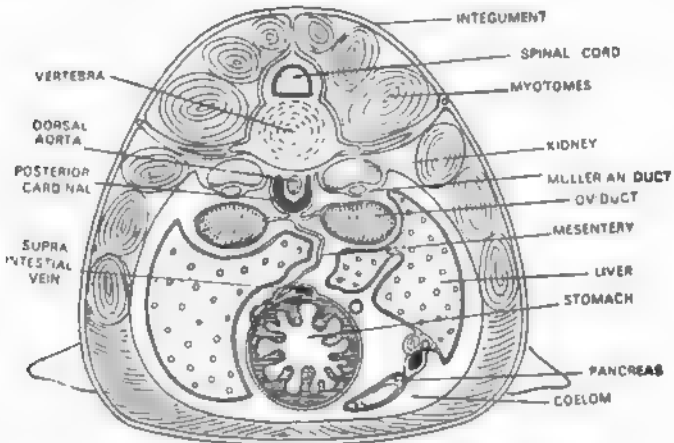


Fig. 3.31. A cross-section of the dogfish passing through the stomach region.

Glands of Digestive System. The liver has already been described earlier. Its right lobe carries the gall-bladder. The bile duct leaves the gall-bladder between the two lobes of the liver, almost in the median plane. It is about half an inch on the whole. It receives ducts from the lobes of the liver. The pancreas as described above, lies in the fold of the stomach and intestine. The pancreatic duct runs forward through the pancreas, close to its ventral border, enters the ventral wall of the intestine, runs along it for about half an inch, and opens just to the outer side of the line of attachment of the spiral valve. The rectal or caecal gland is a short thick-walled tube lying in the abdominal cavity dorsal to the rectum.

The spleen is a large gland consisting of two lobes one extending along the outer curvature of the cardiac stomach while the other lying parallel to the pyloric stomach. The thyroid is an irregular mass of glandular tissue surrounded by a connective tissue capsule lying just behind the symphysis of the lower jaw, ventral to the basihyal cartilage. The thymus appears as a series of nodules connected into a chain above the gill-pouches only in the embryo.

Physiology of Digestion. Apparently no digestion goes on in the mouth and pharynx. The teeth are not meant to bite. Probably the teeth may be used for tearing the food. They, however, prevent the escape of the prey. The wall of the pharynx is lined by a stratified type of epithelium into which numerous mucous glands open. The secretion of the glands has no digestive function, strictly speaking, it simply helps in the passage of food. The salivary glands of higher vertebrates, doubtless, originate as a result of modification of the mucous glands of the pharynx. Digestion begins in the stomach which functions like that of higher vertebrates. The gastric juice secreted by the

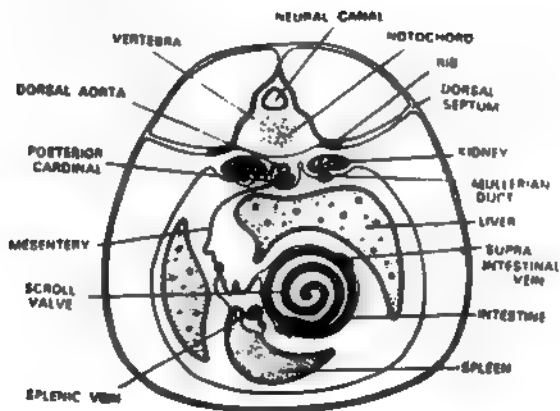


Fig. 3.32. Cross-section of the dogfish passing through the intestinal region showing the scroll-valve.

stomach contains hydrochloric acid and pepsin that converts proteins into peptones. The gastric juice is not able to digest chitin. The pyloric stomach has no digestive activity of its own. The bile and pancreatic duct opens into the stomach beyond the pyloric sphincter. The bile juice functions as in higher forms and the pancreas secretes typsinogen but may also secrete trypsin. It also secretes starch-splitting ferment amylopsin and the fat-splitting ferment lipase. The small intestine has greatly increased internal surface due to the scroll valve. Presumably absorption takes place wholly in this organ. The rectum is short and the rectal glands are of unknown function. Little is known about the function of the liver in fishes but probably it functions as in other forms. It serves as a storing organ and probably also plays a part in destruction of red blood corpuscles.

RESPIRATORY SYSTEM

Dog-fish. *Scoliodon*, breathes by means of gills borne in a series of gill-pouches. There are five pairs of such gill-pouches each of which is compressed antero-posteriorly and communicates with the pharynx by a large internal branchial aperture and with the exterior by a narrow external branchial aperture (Fig. 3.33). The first pair of visceral clefts (between the mandibular and hyoid arches) gives rise to the spiracle, which is vestigial in *Scoliodon*.

The gills are a series of closely set, soft and highly vascular folds of the mucous membrane radiating outwards from the cartilaginous branchial arches and supported by gill-rays. Each gill-pouch has two rows of gill-lamellae, one on its anterior and the other on its posterior wall. Successive gill-pouches are separated from one another by stout fibromuscular partitions, the internal branchial septa, the inner border of each encloses a visceral arch with its branchial rays. There are many types of gills. The holobranch (Fig. 3.34) or complete gill consists of two sets of lamellae attached to a visceral arch and its inter-branchial septum. First four branchial pouches bear holobranchs. The demibranch or a half-gill comprises only a single set of lamellae. Such a gill is borne by the hyoid arch on its posterior border. The pseudobranch is a rudimentary gill, consisting of about half a dozen small parallel folds, on the anterior wall of the spiracle but in *Scoliodon* the spiracle bears no gill-lamellae. The form, of gill is lamelliform. In this the gill-folds are attached along their length to the inter-branchial septum. In bony fishes (teleosts) the gills are filiform or pectinate.

There is an extensive system of sinusoids within each gill-lamella. These receive

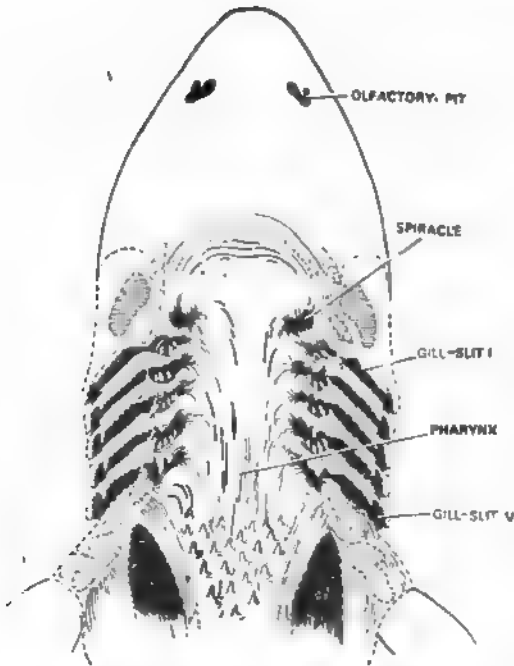


Fig. 3.33. The pharynx exposed to show the gill-pouches.

blood from the afferent branchial vessels (running along the outer side of the arch) and pass it to the efferent branchial loop at the side of arch. Oxygenation takes place while the blood passes through the network of blood vessels.

Elaasmobranchs and Holocephalan gills. The gills of elasmobranch fishes (sharks and dogfishes) are lateral in position, but ventral in flattened skates and rays. They open independently to the outside and are separated from each other by branchial septa. On either side of the branchial septum is located a set of filaments or demibranch. A septum and its two demibranchs together make up a gill or holobranch. Along the inner margins of the gill-arches are finger-like projections, the gill-rakers (Fig. 3.34) which not only keep food from entering the slits but also aid in directing it into the oesophagus.

The walls of the spiracles are not provided with true gills but in some cases may support a "false gill" or pseudobranch. It is called "false" because its blood supply is not derived directly from an afferent branchial artery but from an efferent branchial artery of the following gill arch which brings oxygenated blood. In bottom feeding skates and rays the spiracles open dorsally instead of ventrally as the other pharyngeal gill-slits do. The spiracles are used to take water in for respiration. Certain larval elasmobranchs which undergo considerable development within the eggshell before hatching have gill-filaments so long that they hang out of the gill-slits as temporary "external gills."

The holocephalans possess only four pairs of gill-slits that are covered by an operculum, which is a flap of integument developed on either side extending backward

from the margin of the hyoid arch until it covers the external openings of the three-anterior pairs of gill-slits leaving only the last pair open to the exterior directly. Probably the forerunner of this opercular flap is seen in the elasmobranch, *Chlamydoselachus*, where the skin on the anterior margin of each gill-slit extends backwards as a small independent protective fold covering the opening of each gill-slit separately.

In all bony fishes the gills are covered with an operculum that is stiffened by flat skeletal plates between the two surfaces of folded integument. The gill-system of ganoids in some ways represents a connective link between that of elasmobranchs and teleostean fishes. Most Chondrostei still have nine pairs of demibranchs but nearly all the Holosteii lose the most anterior pair so that they are limited to eight pairs of demibranchs (four pairs of complete gills). Outside and anterior to the operculum on either side there is a degenerate spiracle in some of the ganoids, while on the inner surface of the operculum there is attached a small opercular gill which is not homologous either with true gills or with the pseudobranchs of the hyoid arch. The interbranchial septa in ganoids are reduced so that the demibranchs placed upon them back to back are no longer in separate individual chambers but occupy a common branchial cavity (Fig. 3.34).

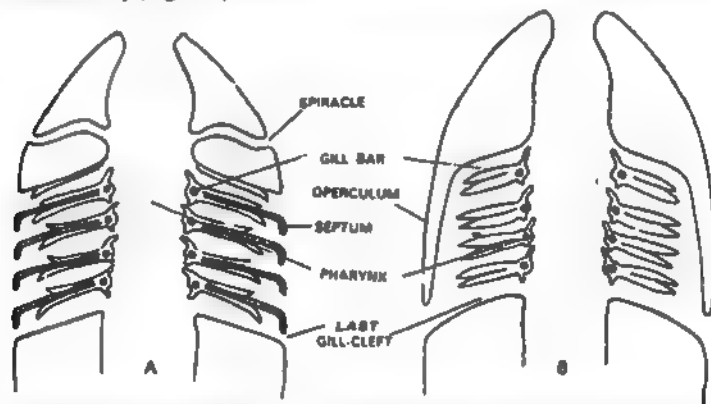


Fig. 3.34. Gills and branchial chamber in an elasmobranch fish (A), and a teleost (B), showing gill-septa in the former.

The reduction of the outer branchial septa becomes complete in teleosts so that all the gills lie closely compacted in a common chamber covered by the operculum. The number of gill arches in both ganoids and teleosts is usually four or five pairs, although in some bony fishes they may be reduced to three or even two pairs. Spiracles are not characteristic of teleosts. In fishes like eels the opercular opening is much reduced so that water can be retained in the branchial chamber under unfavourable conditions.

The three genera of the Dipnoi have different arrangement of gills. *Neoceratodus* has four pairs of gills, *Lepidosiren* three, and *Protopterus* two. Spiracles are present in the embryonic stage, not only in the adults. Larval stages of *Lepidosiren* and *Protopterus* have additional four pairs of external gills of the pinnate (pinna, feather type).

Mechanism of Respiration. In order to maintain a continuous supply of oxygen for respiration, a current of water is maintained, through the gill-pouches by the movements of pharyngeal wall. Water enters the bucco-pharyngeal cavity through the mouth (and perhaps also through the spiracle). For this the floor of the pharynx is lowered with the help of hypobranchial muscles such as the coraco-hyoid and coraco-branchials, and mouth is opened. The increased volume-capacity of the bucco-pharyngeal cavity draws water in. Now the mouth closes and the floor is raised. The

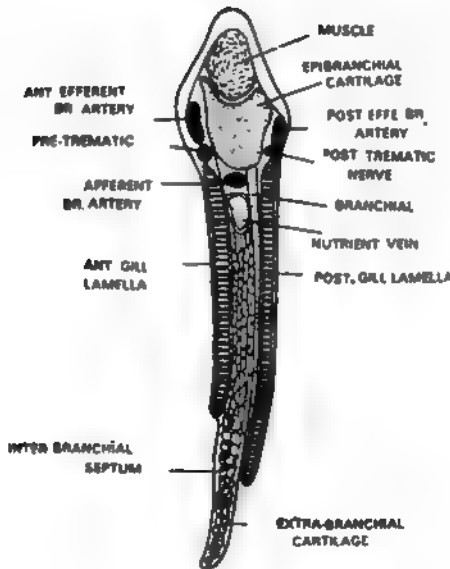


Fig. 3.35. Horizontal section of a holobranch.

contained water, consequently, is forced through the internal opening of the branchial clefts into the gill-pouches (the entrance of the oesophagus is already closed by the contraction of its muscles). The water bathes the gill-lamellae and then passes out through the external gill slits. The buccopharyngeal i.e., cavity acts as a force pump that maintains a current of water only in one direction, i.e., in through the mouth and out through the gill-slits. Along the anterior border of each gill-slit there are flaps of skin which prevent the entry of water through the slits when the mouth is open and the pharynx enlarging. Likewise, when the pharynx contracts the water is prevented from rushing out by the lips that seal the mouth, when it is closed. By the alternate contractions and relaxations of their intrinsic musculature the gill-pouches also contract and relax, thus aiding in the maintenance of water current.

The water that enters the gill-pouch carries a large amount of dissolved oxygen. The capillary walls that separate this oxygen from blood are very thin and permeable. Thus the oxygen dissolved in water passes through the thin wall of the blood vessels by *endoosmosis*, and carbon dioxide of the blood passes out by *exosmosis*, into the water. The carbon dioxide is got rid of by the outgoing respiratory current and oxygen picked up by the blood and transported to different parts of the body. Therefore it is evident that the respiratory system is solely concerned with 'breathing' which is sometimes called. The external respiration oxygen free or dissolved in water is taken by blood at some respiratory surface (gill or lung) and conducted to different parts of the body. The result of the respiratory activities is the release of energy within the tissue. It is called *tissue respiration*. The energy is released as a result of complex chemical reactions, each of which is catalysed by a special respiratory enzyme within the protoplasm of the tissue. The energy is provided by the oxidation of certain chemical compound called the *substrate*. In many instances the substrate is glucose, itself, but as a rule, the substrate is only in part derived from the glucose, brought to the tissues by the blood. Within the tissues the glucose is in dilute aqueous solution and its simple oxidation (as in the laboratory) is not possible. Furthermore, the oxidation must take

place at the relatively low temperature of the body. The oxidation within the tissue, as such, is a complicated process the end product of which is carbon dioxide, water and energy.

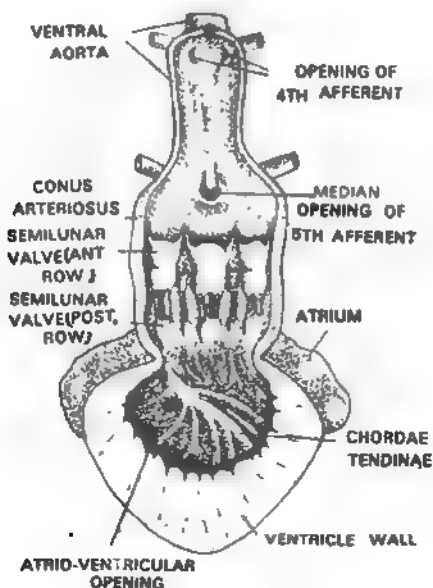


Fig. 3.36. Dissection of the heart of *Scollodon*.

VASCULAR SYSTEM

The blood vascular system comprises the blood the conducting channels or blood vessels (arterial and venous systems) and the heart, located within the pericardial

Heart. The heart lies in the pericardial cavity, which is a median triangular cavity lying between the gills with the apex directed forwards, and is almost completely occupied by the heart. The heart is a single muscular tube bent on itself forming four chambers, each separated from the other by a transverse constriction. The sinus venosus is a triangular thin-walled chamber elongated transversely, attached, along whole length, to the posterior and dorsal wall of the pericardial cavity. Laterally it receives two large veins, the duct Cuvieri, and hepatic sinuses open into it in the postero-median line. Anteriorly the sinus opens into the atrium (Fig. 3.36) by a median aperture, the sinu-atrial aperture, guarded by two membranous valves. The atrium (auricle) is a large sac occupying the dorsal half of the pericardial cavity. Its walls are thicker than those of the sinus venosus. It is triangular in shape, with its posterior angles produced into processes which project laterally at the sides of the ventricle in its natural position. It opens into the ventricle by the atrio-ventricular aperture, guarded by a bilabiate valve. The ventricle is the most conspicuous chamber of the heart. It has thick-muscular walls, the inner surface of which is produced into numerous muscular strands, giving it a spongy texture (Fig. 3.36). Ventrally the ventricle is supported by the coracoid cartilages. The conus arteriosus is a stout muscular tube running forwards from the ventricle to the anterior end of the pericardial cavity. The inner wall

of the **conus arteriosus** is provided with two transverse rows of semilunar valves, each row containing three valves, one dorsal and two ventrolateral. The free-ends of the valves are connected to the walls of the ventricle by **tendinous cords** to keep them (valves) in position.

Development of Heart. The heart of vertebrates is the central organ for maintaining the circulation of the blood. It lies in the **pericardial cavity** the walls of which constitute the **pericardium**. The vertebrate heart is essentially a modified blood vessel half artery and half vein. It consists of two kinds of chambers, a thin-walled **venous chamber** (receiving chamber) where the returning blood collects and a thick-walled **muscular arterial chamber** (forwarding chamber) separated from the former by valves which prevent the retreat of the blood when the muscular walls contract. The heart has largely muscular walls. The outer layer or **epicardium** is really pericardial in nature, the central layer consists of cardiac muscles and is called **myocardium**, while the innermost layer lining the blood cavity is called the **endocardium**.

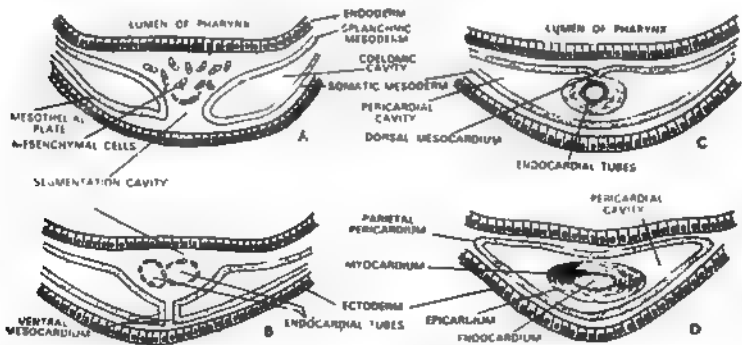


Fig. 3.37. Stages in the embryonic development of the heart. A, mesenchymal cells accumulating above the ventrally meeting mesodermal plates; B, the mesenchymal cells have formed a pair of endocardial tubes (in the frog and others a single tube alone is formed); C, the endocardial tubes unite to form a single tube, the lateral plates have met, ventral walls between the two plates have disappeared, dorsal mesocardium suspends, the cardiac tube; D, the dorsal mesocardium has disappeared and a pericardial cavity is formed

The heart always arises as a simple tube of splanchnic mesoderm and during its formation becomes enclosed in a special portion of the coelom the **pericardial cavity** bounded by coelomic epithelium forming the **pericardium**. The vertebrate heart appears beneath the pharynx. Between the pharyngeal endoderm and splanchnic mesoderm a group of cells appears in the midventral line. These are the cells destined to form the epithelial lining **endothelium** of the heart. These cells eventually become arranged in the form of a tube¹ and at the same time the splanchnic mesoderm becomes folded longitudinally around the endothelial tube. The upper edges of the mesodermal folds meet and fuse to form a tube from which ultimately arise the **myocardium** (the muscular part of the heart) and also the **epicardium** (the delicate investing layer). This is the **cardiac tube** which becomes suspended in the cavity that has now become cut off from the rest of the coelom to form the **pericardial cavity**, by a dorsal mesentery (**dorsal mesocardium**).

Anteriorly and posteriorly the edges of the cardiac plate do not come together, but they roll up separately to produce each a tube connected with the cardiac tube. The anterior pair forms the **mandibular arteries**, the posterior pair the **omphalomesenteric veins**. At the level of the posterior limit of the cardiac tube arises, on either side, a transversely disposed tube, the **ductus Cuvieri** which joins the cardiac tube. The Cuvierian duct separates off the pericardium from the coelom behind.

¹ In the vertebrates with relatively small yolk two tubes are formed and soon both fuse to form one.

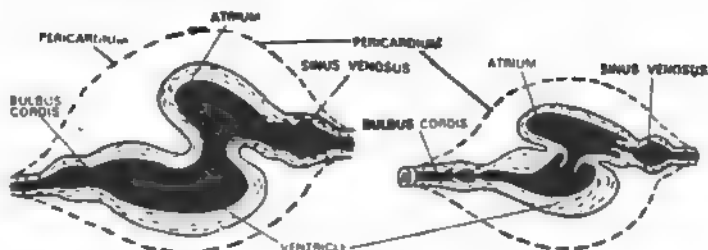


Fig. 3.38. Twisting of the tube begins (A) and internally valves have also been formed (B).

This straight tube is contained within the circumscribed space of the pericardial cavity. Its ends are fixed as such as it increases in length. It becomes twisted into a characteristic S-shaped curve. Internally the lumen becomes divided into chambers by the development of the **valves**. These valves are formed by reduplication of the lining membrane with some inclusions from the wall (Fig. 3.38 B).

Externally some constrictions appear due to the differential thickening of the myocardium. In this way a simple heart is formed consisting of four chambers (Fig. 3.38), the contractile **sinus venosus**, into which the main veins of the body open; the **atrium** which receives blood from the sinus venosus and is slightly muscular, the **ventricle** which is very muscular and receives the blood from the atrium, and **bulbus cordis** which is also muscular though not to the same extent as the ventricle. Blood from ventricle passes into the bulbus cordis to be distributed to the arteries.

Arterial System. This is the set of blood vessels taking blood away from the heart. In the dogfish, as in other fishes, a set of blood vessels, the **afferent branchial arteries**, takes the blood to the gills, and another set, the **efferent branchial arteries**, collects it from the gills and conducts to the different parts of the body.

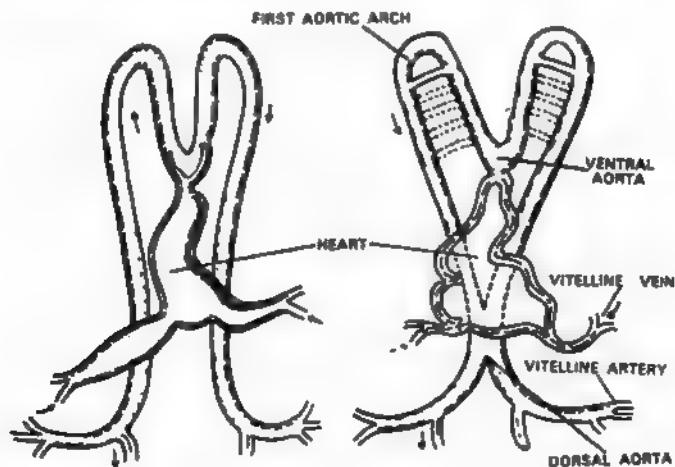


Fig. 3.39. Further twisting of the cardiac tube and formation of the mandibular arteries and vitelline veins.

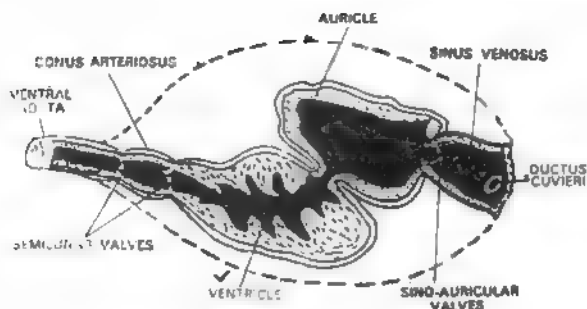


Fig. 3.40. Heart of the dogfish.

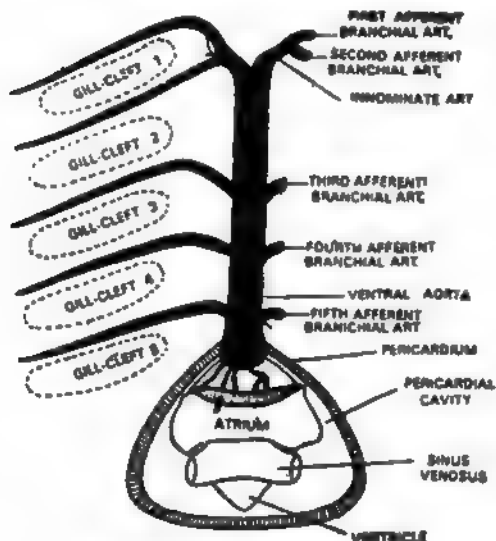


Fig. 3.41. Heart and the afferent arteries of the dogfish.

ARTERIAL ARCHES

In true vertebrates the number of pairs of branchial loops, although less in the adult, is typically six during embryonic development. Certain primitive sharks, e.g., *Hexanchus* has seven and some cyclostomes more. The **mandibular arteries** (first aortic arches) pass upwards on either side of the pharynx and then turn backwards forming a pair of longitudinal tubes, dorsal to the alimentary tract. These are called the **radices aortae**, which secondarily join to make the main dorsal aorta. As these developments take place other **aortic arches** are also laid down between the mandibular arteries and the pericardium. These connect the ventral aorta with the radices aortae and run in the region of the visceral clefts. The history of these arches differs greatly in different classes. Usually there is a reduction in the number of the arches. Some are completely

lost, whereas, others become specially modified accompanying changes in the respiratory system.

In the fishes, with the development of gills, each aortic arch becomes divided up into two portions. (1) an **afferent** portion conveying blood from the ventral aorta to the gills, and (2) an **efferent branchial artery** associated with the **radix aortae**. These two vessels parallel each other for a part of their course and are connected with each other by numerous **capillary loops**, which run through the gill-filaments. In passing through the gills the blood loses its carbon dioxide and takes up oxygen and thus becomes changed from venous to arterial blood. In the amniotes afferent and efferent branchial arteries are continuous from the ventral aorta to the **radices aortae**.

In *Selachii* the afferent branchial arteries retain their original relation to the gill-arches, the efferent vessels are related to the gill-slits. In teleosts the efferent branchial vessels remain connected with the gill-arches like the afferent. In some teleosts the two roots of the dorsal aorta may remain widely separate in the branchial region (e.g., in *Gadus morhua*).

The first of the arches (the mandibular) never forms afferent and efferent portions since no gills are ever developed in their region. From each half of this arch an artery, the **external carotid**, extends forwards to supply the lower and a part of upper jaw, while an **internal carotid artery** (Fig. 3.42) forms an extension forward of each radix and supplies the brain and face. Later their relations are such that the carotids appear to arise from the first of the functional arches. In fishes in general the two most anterior pairs of loops that are supported by the mandibular and hyoid arches suffer a great change. They become converted into branches of the third in adult life, leaving the remaining four to become **branchial arches**, interrupted by the capillaries of the internal gill.

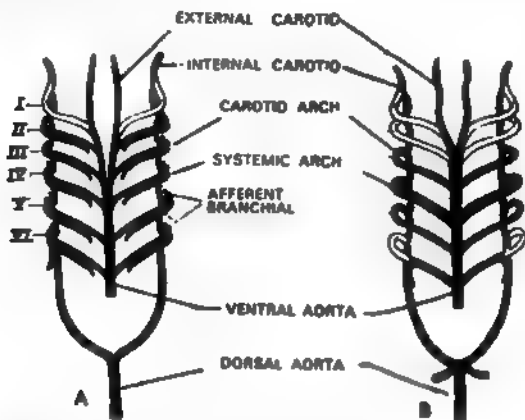


Fig. 3.42. Fate of the aortic arches. A, fish; B, amphibian.

Afferent Branchial. The ventral aorta is the name given to the anterior prolongation of conus arteriosus. Passing through the pericardium it extends along the ventral surface of the pharynx right up to the posterior border of the hyoid arch, where it bifurcates into two branches, the **innominate arteries**, each of which again divides into two forming first and second **afferent branchial arteries** (Fig. 3.35). The anterior branch of the innominate artery is the first afferent branchial, it runs along the posterior border of the hyoid arch and supplies the gill-lamellae of hyoidean demi-branch. The second afferent branchial supplies arterial branches to the anterior and posterior gill-lamellae of the first branchial arch. The third afferent branchial arises a little behind the bifurcation of the ventral aorta and supplies the second branchial

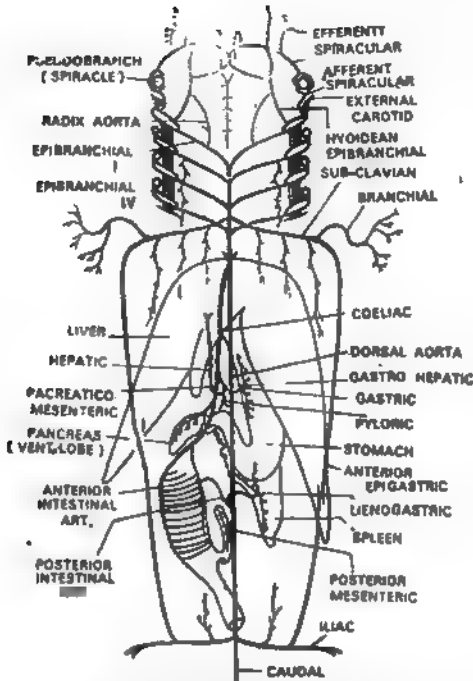


Fig. 3.43. Entire arterial system of the dogfish.

arch. The fourth and fifth afferent branchials arise almost equidistant from one another from the ventral aorta and run along the outer borders of the third and fourth branchial arches, breaking into the gills of the region.

Efferent Branchial Arteries. The blood from the gills is collected by four loops of blood vessels around the four branchial clefts on each side. Besides these a single vessel collects blood from the fifth branchial cleft. The four loops and the independent single vessel form nine efferent branchial arteries. The four loops are connected with one another by short longitudinal connectives running across the inter-branchial septa. Likewise the last vessel of the half loop is also connected with the blood vessels of its side (a part of loop surrounding the fourth gill-cleft). The loops are further connected with each other by a net-work of longitudinal commissural vessels between their ventral extremities.

The efferent branchial arteries are nine in number (eight formed by four collector loops and the independent ninth). They run along the anterior and posterior borders of the five gill-clefts. The epibranchial arteries are four on each side. Each of the collector loops is continued into an epibranchial artery which runs backwards and inwards to the mid-dorsal line meeting to form the dorsal aorta. The half-loop has no epibranchial of its own. The dorsal aorta is formed by the union of the four pairs of the epibranchials, and runs backwards along the whole length of the body. Anteriorly it runs a little distance and then bifurcates into two branches, the lateral aortae.¹

¹ The blood vessels arising anteriorly supply the brain and associated organs. Different terminology has been used to describe these blood vessels by different workers. This nomenclature does not agree with that used in higher vertebrates. The brain, however, receives blood from the two branches of the dorsal aorta and from others arising from the first efferent branchial.

Arteries of the head. The first efferent branchial or **hyoidean efferent** supplies blood to the head, though a little is also contributed by the anterior end of the dorsal aorta. Three large vessels arise from the efferent hyoidean of each side and carry blood to the head (Fig. 3.44)

The **external carotid artery** is a large vessel arising at anteroventral corner of hyoidean efferent. Anteriorly it travels to the hyoid arch and divides into two branches: (a) The **ventral mandibular** supplying the mandibular region, and (b) the **superficial hyoid** supplying the skin and subcutaneous tissues over the ventral part of the hyoid arch. The **efferent spiracular (spiracular epibranchial) artery** (Fig. 3.44) arises at about the middle of the hyoidean efferent. It runs forwards on the outer side

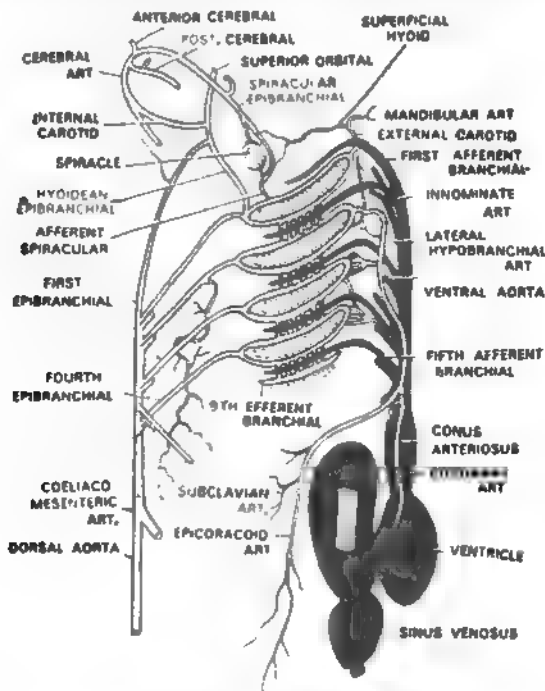


Fig. 3.44. Afferent and efferent arteries of the dogfish.

of the hyomandibular and epibranchial artery across the floor of the orbit and enters the cranial cavity through a small foramen. Before entering the cranium it gives a branch to eyeball, the **great ophthalmic artery**. Within the cranium it unites immediately with a branch of the **internal carotid** to form a short vessel, the **cerebral artery** soon bifurcating to form **anterior and posterior cerebral arteries**. The **hyoidean epibranchial** (Fig. 3.43) artery arises at the other end of the first efferent, a little before its fusion with the second efferent to form the **first epibranchial**. It runs forwards and inwards to the posterior border of the orbit where it is joined by the anterior branch of the dorsal aorta and immediately divides into two branches, the **stapedial** and the **internal carotid**. The **stapedial artery** runs forwards and enters the orbit where it gives two branches, one supplying the eye-muscles, and the **superficial hyoid** supplying the skin and subcutaneous tissues in the region above the auditory capsules, and other supplying the anterior boundary of the orbit.

The former is called the *inferior orbital* while the latter is the *superior orbital*. The internal carotid passes inwards to the buccal cavity and enters the cranium where it divides into two branches, one of which unites with its fellow of the opposite side forming a loop, while the other unites with the stapedia to form the anterior and posterior cerebral arteries.

The *dorsal aorta* is formed by the union of the four pairs of the epibranchial arteries. It runs backwards along the whole length of the body, lying beneath the vertebral column in the trunk. In the tail region it continues into the haemal canal of the tail vertebrae as the *caudal artery*. The following are the principal branches of the dorsal aorta.

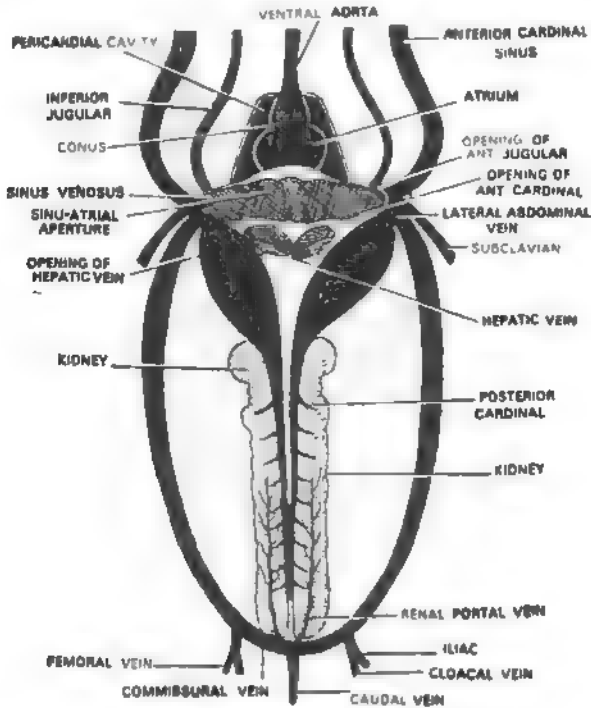


Fig. 3.45. Venous system of *Scoliodon*.

The *sub-clavian* (Fig. 3.43) arteries are a pair of vessels arising close to the union of four epibranchial arteries. They run outwards and backwards to the pectoral girdle and the pectoral fin of either side, which they supply. The *coelaco-mesenteric* is a large median artery arising from the dorsal aorta behind the junction of the fourth pair of epibranchial arteries. It divides into two unequal branches, (a) the *coeliac* that supplies the stomach and liver, etc., and (b) the *anterior mesenteric* supplying the pancreas, the intestine and the rectum. The *lienogastric* artery arises a short distance behind the origin of the coeliac-mesenteric. It is also a median blood vessel giving off branches supplying the genital organs, posterior part of the intestine and the spleen, etc. The *posterior mesenteric* artery is a small median vessel arising from the aorta about an inch and a half behind the lienogastric. It runs backwards to the mesentery and the

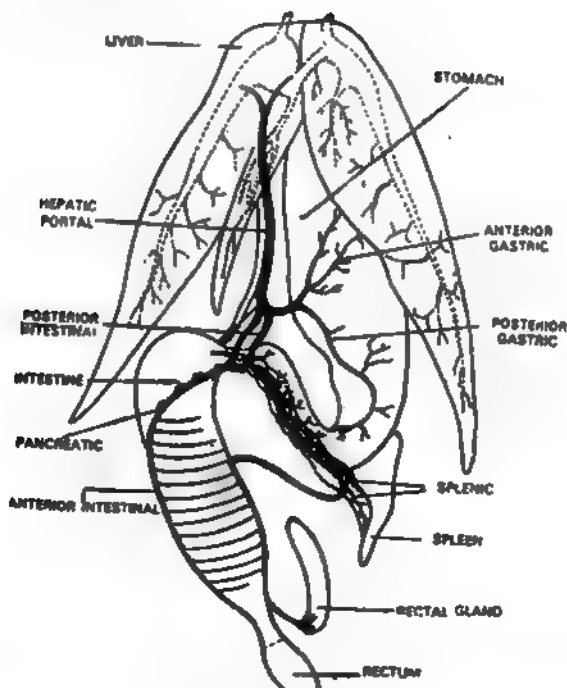


Fig. 3.46. Hepatic portal system of the dogfish.

rectal gland. The **parietal arteries** are a series of paired vessels arising at intervals along the whole length of the aorta and supplying the body wall. The **renal arteries** are small paired vessels arising from the parietal arteries and supplying the kidneys, which they enter from the dorsal surface. The **iliac arteries** are a pair of vessels similar to the parietals, each of them extending into the pelvic fin.

Venous system. The blood in the dog-fish is not returned by narrow tubular veins but by large spaces or **sinuses** (Fig. 3.45). The **anterior cardinal sinuses** collect blood from the outer side of the head and the branchial region. Each is a large sinus running backwards between the dorsal end of the gill-pouches and the muscles of the body wall. Posteriorly it enters the Cuvierian sinus. It collects blood from the orbit, the nasal region and the hyoidean region. The **inferior jugular sinuses** are a pair, running parallel and ventrally to the anterior cardinal sinuses, and each collects blood from the sides of the lower jaw and the ventral region of the gill-pouches. It commences just in front of the posteroventral margin of the first gill-cleft and is situated beneath the floor of the buccal cavity and pharynx. Posteriorly it opens into the Cuvierian sinus. The posterior cardinal sinuses lie close together along the roof of the abdominal cavity. They originate in between the kidneys, along the posterior region of which only a median **inter-renal vein** represents these, but in the anterior region of the kidneys the right and the left posterior cardinal sinuses are distinct. In the region of the oesophagus each of them expands into a wide thin-walled sac opening finally into the Cuvierian sinus. The **hepatic sinuses** are two large thin sinuses collecting blood from the lobes of the liver. After traversing the whole length of the right and left lobes of the liver they open anteriorly into the sinus venosus by two apertures in the median line.

The Cuvierian sinuses are a pair, each of which runs transversely, like its fellow of the opposite side, passes through the pericardium and opens into the basal angle of the sinus venosus.

Development. The development of veins given here applies to that of elasmobranch fishes. Basically it is similar in all vertebrates, the differences are dealt with in the portion dealing with evolution of veins. At the posterior end of the cardiac tube two blood vessels, the *omphalomesenteric* or *vitelline* veins, (Fig. 3.46 A) are formed. They extend back from the heart, around the liver to meet the extensions of the *omphalomesenteric* arteries. Another vein, the *subintestinal* vein¹, develops along the ventral side of the posterior part of the alimentary canal and gets connected with the left vitelline vein. It forms a loop around the cloacal region (Fig. 3.46 B) and continues behind as the *caudal* vein. By this time venous vessels are laid down in the head and in the trunk region posterior to the heart. These are called the *anterior cardinal* and the *posterior cardinal* respectively. The anterior and posterior cardinals of each side meet to form paired *common cardinals* or *ducts* of Cuvier that open in the sinus venosus. By this time liver grows and engulfs² the veins around it which ultimately break up into a capillary in the liver. This establishes a *hepatic portal* system consisting of a separate *hepatic portal* trunk posteriorly and *hepatic* veins anteriorly (representing the remaining portions of the vitelline veins). The *subclavian* vein is the next new blood vessel to arise from the anterior fin-buds to the common cardinals (Fig. 3.46 C). The subclavians receive the *ventral abdominal* veins from the ventral abdominal wall. All this time the posterior cardinals keep growing backwards and meet the cloacal loop. Now the subintestinal breaks off from the cloacal loop and forms the *hepatic portal* vein. It collects blood only from the region of the gut and conducts to the heart through the capillary network in the liver. The blood collected by the caudal vein from the posterior part of the body now reaches the heart through the posterior and common cardinals.

Next a pair of *subcardinal* veins develop along the inner margins of the growing kidneys (*mesonephros*). Between the sub-cardinal and the corresponding part of the posterior cardinal some lateral connections appear (Fig. 3.47 F). The tissue of the growing kidney grows over these lateral connections with the result that they break up into capillaries, excepting the most anterior one. Now the part of the posterior cardinal just posterior to the first lateral connection disappears (Fig. 3.47 G) and the anterior part of the posterior cardinals separates from the posterior part. The blood from the tail end of the body must pass through the capillary network in the kidney (*renal portal* system) before reaching the heart through the anterior portion of the posterior cardinals and the common cardinals. Meanwhile blood vessels originating in the posterior fin-buds, the *iliac* veins, become connected with the ventral abdominals.

The portal systems are two and quite well represented. The *hepatic portal* vein (Fig. 3.46), is formed by the union of the veins from the various parts of the alimentary canal. It divides into three branches before entering into the liver lobes. The *renal portal* system consists of two *renal portal* veins formed by the bifurcation of the caudal vein, each of which after running on the inner side of the kidneys, breaks up into capillaries in the substance of the kidneys. The blood is then collected by the *renal* veins which open into the hinder portion of the posterior cardinal sinus.

NEURO-SENSORY SYSTEMS

The *neuro-sensory* system of the dogfish includes the *nervous system* and organs of *special sense*. The nervous system comprises the central nervous system consisting of the brain and the spinal cord and a peripheral nervous system including the cranial and spinal nerves.

Brain. The dogfish lives in deep seas and naturally, depends more upon the sense of

¹ In some cases a pair of subintestinal vessels are formed and soon they fuse to form a single median vessel.

² Some authors have described the formation of two venous rings by the anastomosis of the vitelline veins. The growing liver pushes into the anterior vitelline loop and breaks it into capillaries.

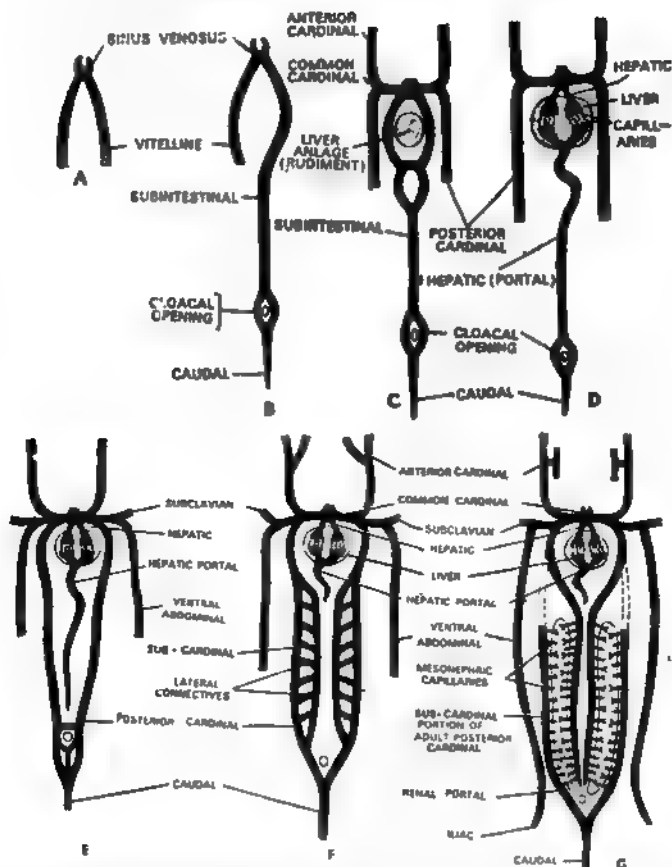


Fig. 3.47. Development of veins in elasmobranch fish, diagrammatic, A, vitelline stage; B, subintestinal stage; C, common cardinal stage; D, hepatic portal stage; E, subclavian stage; F, subcardinal stage; G, renal portal stage (after Hochstetter and Hyman).

smell than upon the sense of sight. The powerful movements during swimming also necessitate efficient control of muscular activity. The brain, therefore, is specially modified to accommodate these activities. The olfactory lobes (Fig. 3.48) and the cerebellum are well developed, whereas, the optic lobes are not enlarged. The fore-brain is represented by the relatively enormous olfactory lobes which are closely applied to the olfactory organs. The pallium merely consists of small paired protuberances on the dorsal surface of this region (Fig. 3.48). The thalamencephalon narrows from the wide anterior portion. Dorsally it carries the pineal body lying closely against the roof of the cranium. The greater part of its dorsal surface is occupied by the anterior choroid plexus. Ventrally the thalamencephalon has the optic chiasma and a relatively large pituitary body, the latter consisting of the infundibulum, hypophysis and the accessory lobi inferiores of the infundibulum. The mid-brain is very moderately developed. Dorsally there are two rounded prominences which project some-

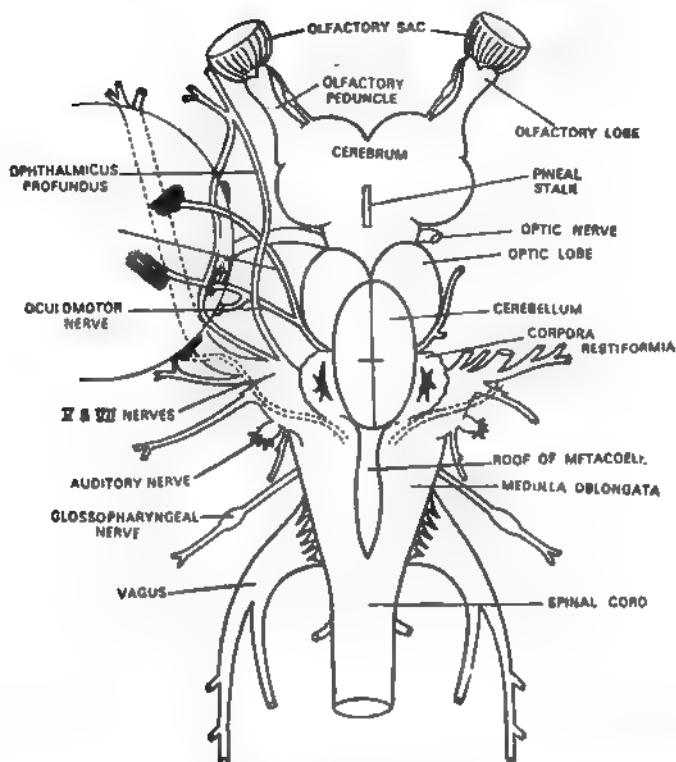


Fig. 3.48. Brain of the dogfish, dorsal view.

what beyond the sides of the brain. These are the optic lobes (*corpora bigemina*). Ventrally the *crura cerebri* are hidden by the posterior part of the pituitary body. The hind-brain has a very prominent cerebellum that projects forwards, to some extent covering the optic lobes, and backwards over the roof of the fourth ventricle. The cerebellum continues in the *medulla oblongata* that is very well developed.

Ventricles (Fig. 3.50). The cavity of each olfactory lobe is known as *rhinocoel* which communicates with the lateral ventricles behind. The lateral ventricles open into the large third ventricle behind, each by the *foramen of Monro*. The cavity of the third ventricle extends into the infundibulum of the pituitary body and also into the base of the pineal stalk. The optic lobes have *optocoel* within them. The fourth ventricle is the cavity of the medulla into which also opens the cavity of the cerebellum. A common space connecting the third and fourth ventricles, into which the *optocoel*s also open, is called the *ter*.

THE CENTRAL NERVOUS SYSTEM

Development. In the dorsal surface of the embryo a special tract of ectoderm is differentiated. This is called the *neural or medullary plate*. By a process of differential growth and migration of cells the edges of the plate become raised up into

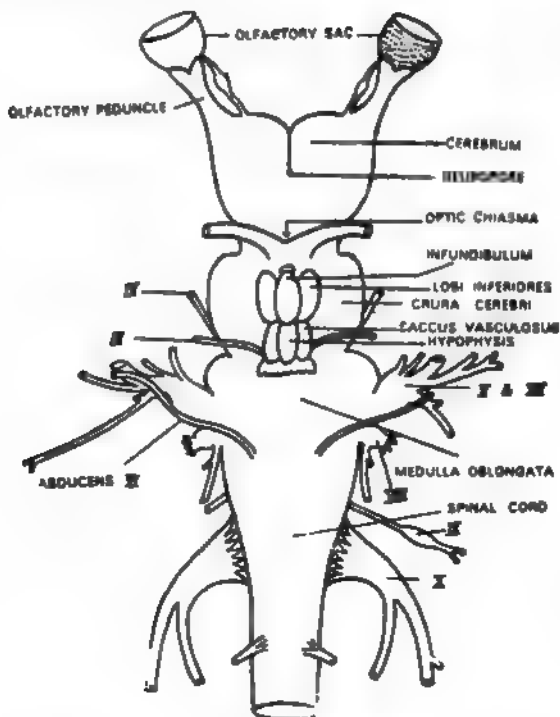


Fig. 3.49. Brain of the dogfish, ventral view.

folds, the neural folds (Fig. 3.51). The neural folds approach each other, as the development proceeds transforming the neural plate into neural groove in the middle line. Eventually the folds fuse forming the neural tube in the mid-dorsal line lying immediately beneath the now reformed outer surface (Fig. 3.51 D) and above the notochord (shown by smaller circle below the neural tube). The fusion of the neural folds is not complete along the whole length of the neural groove, a small opening, the neuropore, is left out on the anterior side. Through this the neuropore communicates with the exterior. The neuropore persists only for some time and closes ultimately. It may not occur in all cases. Posteriorly the neural tube may communicate temporarily with the archenteron by the neurenteric canal. The neural tube is a simple tubular structure usually wider towards the anterior side. This is so because the anterior part of

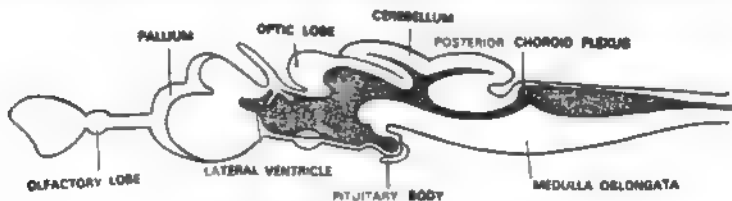


Fig. 3.50. Sagittal section of the brain of the dogfish.

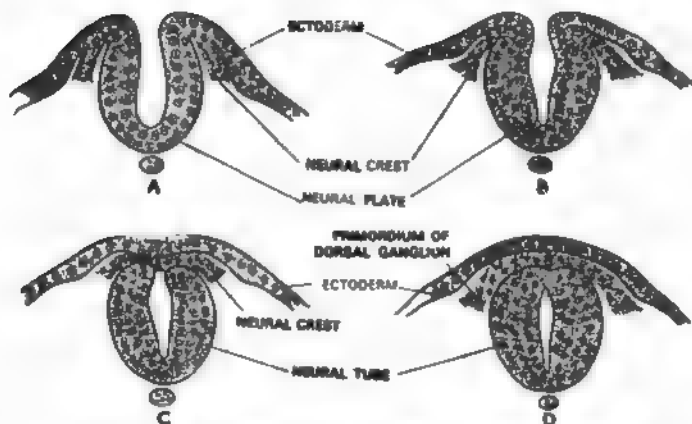


Fig. 3.51. Transverse sections of the embryo to show the formation of the neural tube. A and B show invaginated neural plates; C incomplete and D complete neural tube.

the neural plate is wider than the more posterior part, and it is this wider part that forms the wider tube that ultimately gives rise to the brain and the remaining posterior part forms the spinal cord.

Brain. The brain is the anterior part of the central nervous system present in all bilaterally symmetrical animals. In response to the aggregation of sense organs in the head region the brain becomes enlarged and differentiated to varying degrees. The first step in the differentiation of the brain is that the anterior wider part becomes moulded into three dilated regions called the three **primary cerebral vesicles**. This moulding is the result of differential growth of the tissue of the tube. Of the three vesicles the first is called the **fore-brain**, the middle one is the **mid-brain** and the hinder one is the **hind-brain**. These three primary cerebral vesicles give rise to the various parts of the brain by thickenings and foldings, etc.

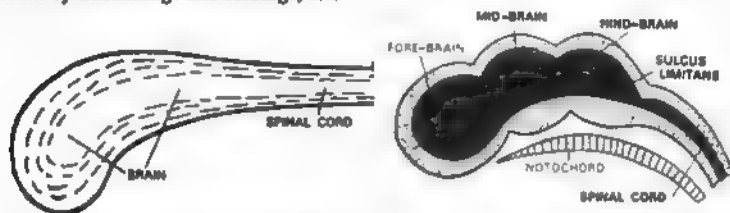


Fig. 3.52. A, side view of the anterior end of the entire neural tube; B, longitudinal section of the neural tube at a slightly advanced stage showing the formation of three primary cerebral vesicles.

Fore-Brain. The **fore-brain** or **prosencephalon** is the anterior-most of the three divisions marked out in the embryonic brain of the vertebrates by constriction. During further development it gives rise to cerebral hemispheres, eyes, hypothalamus, etc. A further constriction divides the fore-brain into two parts the **telencephalon** anteriorly and the **thalamencephalon** posteriorly. From the telencephalon a lobe grows forward towards each olfactory organ on each side. Each lobe receives nerve fibres growing backwards from the cells of each olfactory organ. These are the **olfactory lobes**. The original anterior wall of the telencephalon forms the **lamina terminalis**; the roof of telencephalon becomes the **pallium** and its ventrolateral wall thickens to form the **corpora striata**. Both the roof and the side walls of the telencephalon later bulge outwards and forwards leaving the lamina terminalis behind. These paired lobes are

the **cerebral hemispheres**, which vary in size in different vertebrates. From the above it is evident that the roof of each cerebral hemisphere is formed by the **pallium** and its ventrolateral wall by a **corpus striatum**, and into each extends the cavity of the embryonic neural tube forming the lateral ventricles (see later). These communicate with the median ventricle by an aperture, the **foramen of Monro**. The cerebral hemispheres become large in higher vertebrates attaining very considerable proportions in the mammals originally mainly concerned with sense of smell but in amniotes general co-ordinating functions become predominant.

The **thalamencephalon** gives rise to outgrowths both dorsally and ventrally and also on the sides. The outgrowth on the dorsal surface forms the **pineal organ** (Fig. 3.53). The outgrowth from the ventral surface is called the **infundibulum**. The infundibulum fuses with **hypophysis**, an upgrowth from the stomodaeum and forms the **pituitary body**. Both these structures are potential nervous structures, but eventually they lose

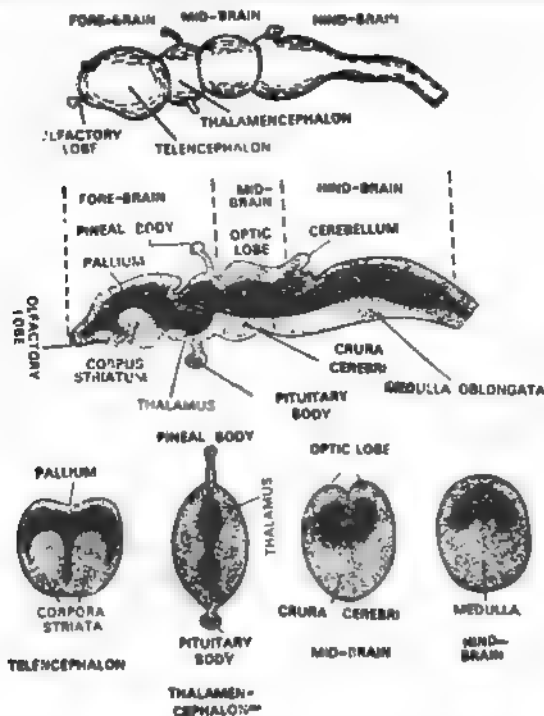


Fig. 3.53. Differentiation of the brain from the three primary vesicles. Entire brain (above), sagittal section (middle), and cross-section through different regions (below). Ventricles are black and cut surfaces stippled.

their nervous character and take up other functions. In lampreys and reptiles the pineal organ assumes the form of an eye and may even be double. But this is so only in some exceptionally rare cases. Generally the pineal organ consists of a knob-like structure lying beneath the roof of the cranium, connected to the thalamencephalon by a slender stalk. The function of the pineal body is not clearly understood in the vertebrates. It is suspected to be an endocrine organ. The pituitary body, on the other hand, is known by a definite notable endocrine organ and secretes hormones which play important role in the animal metabolism.

The cavity of the thalamencephalon is known as the **third ventricle**, its roof remains thin and non-nervous. It becomes much-folded and gets pushed inwards into third ventricle. The covering membrane of the roof is highly vascular and plays an important role in the nourishment of the brain and in the secretion of cerebrospinal fluid. This investing membrane is called the **anterior choroid plexus** and is carried into the third ventricle along with its roof. The sides of the thalamencephalon become thickened forming **thalami**. The thalami give rise to the **primary optic vesicles**, which contribute to the developing eye of the animal.

Mid-Brain. The mid-brain or **mesencephalon** is the middle of divisions marked out by constrictions in the embryonic vertebrate brain. During development its dorsolateral walls become very thick-walled forming the **optic lobes** (or **corpora bigemina** or **tectum opticum**) with small central cavity. The ventral wall also becomes thickened forming a nervous tract linking the thalamencephalon with the hind-brain and is called the **crura cerebri** (**cerebral peduncles**). The roof plate of the mid-brain remains thin. A constriction of the dorsal zone, the **isthmus**, separates sharply the mesencephalon from the hindbrain. In the mammals the optic lobes become transversely divided into four lobes, the **corpora quadrigemina**. On either side the optic lobe is connected with fibres coming from the eye of the opposite side. This forms a crossing of the nerve fibres of the right and left optic nerves called the **optic chiasma**. In lower vertebrates all the nerve fibres of the right optic nerve cross those of the left optic nerve. In mammals on the other hand half of the nerves remain on their original side and half cross. At the anterior end of the dorsal part of the mid-brain there is a band of nerve fibres which crosses from one side to the other. Such cross connections serve to connect the two sides of the central nervous system and are termed **commissures**.

Hind-Brain. The hind-brain or **rhombencephalon** is the hindmost of the three divisions of the embryonic brain. It gives rise to two important parts during development. The dorsal surface of the hind-brain becomes thickened to form the **cerebellum** or **metencephalon**, of varying form and extent in different classes of vertebrates. It is just a transverse commissure in the cyclostomes and becomes a conspicuous part in birds and mammals (with a cortex of grey matter in mammals). It is particularly concerned in the co-ordination of complex muscular movement. The roof of the region behind the cerebellum remains thin and non-nervous and becomes folded and pushed forming the **posterior choroid plexus**. The floor becomes greatly thickened and forms the **pyramids** which pass in front in the cerebral peduncle. The rest of the dorsal zone and the whole of the ventral zone of the hind-brain form the **medulla oblongata** or **myelencephalon**. The medulla passes into the spinal cord, the portion lying behind the posterior limit of the skull, there being no structural difference between the brain and the cord. The primitive function of the medulla is co-ordination of impulses from the lateral line, ear, taste and touch receptors, and it also contains important centres for respiratory movement, control of blood vessels and heart, etc. **Glossopharyngeal** and **vagus** nerves arise from it.

It is evident from the above that out of the three early divisions five regions have been formed. These are the **telencephalon**, **diencephalon**, **mesencephalon**, **metencephalon** and **myelencephalon** and they occur in all vertebrates although vary greatly in different classes (Fig. 3.54). These parts usually retain the derivatives of the original cavity of the neural tube (**neural canal**). The spaces within the brain have been termed **ventricles**.

Cranial Nerves. The first cranial nerve, the **olfactory nerve**, consists of a group of separate fibres, which arise from the olfactory lobes of the brain. The second or the **optic nerve**, innervates the retina. Before entering the orbit, it forms the optic chiasma. The third or the **oculomotor**, the fourth or the **trochlear** and the sixth or the **abducens** supply the muscles of the eye. The eighth or the **auditory** is also a small nerve directly passing from the medulla oblongata to the auditory capsule. The following is the description of the fifth or the **trigeminal**, the seventh or the **facial**, the ninth or the **glossopharyngeal** and the tenth or the **vagus**. The fifth, seventh and eighth nerves arise very close together from the side of the medulla oblongata, all from its widest part, opposite to the posterior part of the cerebellum. The hindermost is the eighth and it passes straight to the auditory capsule. While the fifth and the seventh nerves pass outwards through the skull-wall by a foramen at the posterior and inner angle of the

orbit (Fig. 3.20). The fifth or trigeminal nerve has three main branches. The *ophthalmicus superficialis* is a small branch which enters the orbit along with the *ophthalmicus superficialis* of the seventh nerve and is purely sensory supplying the skin of the snout in front of the olfactory capsule. The *ophthalmicus profundus* arises from the anterior border of the roof of the main nerve, runs forward a short distance within the cranial cavity and there it enters the orbit through a small foramen close to and behind the foramen for the third nerve. In the orbit it passes forward between the dorsal and ventral branches of the third nerve, lying close to the wall of the cranium above the optic nerve and oblique muscles. It passes forward to the olfactory capsule and emerges again through the roof of the olfactory capsule and innervates the skin and dorsal surface of the snout. The fifth or trigeminal appears as a broad ribbon-like band entering the orbit near the outer margin of which it separates into the mandibular and maxillary branch. The maxillary branch is the anterior of the two. It exists in two groups, *superior* and *inferior*, (i) the *superior maxillary* forms a flat ribbon and runs along the floor of the orbit, ventral to the eyeball and eye muscles, and passes over the lower margin of the orbit and innervates the skin of the upper jaw; (ii) the *inferior maxillary* runs directly outward along with the mandibular and turning round the angle of the mouth runs along the lower jaw. It is very superficial, just below the skin, at the place where it crosses the upper jaw. The root of seventh or facial nerve arises immediately behind the fifth and divides into four main branches. The *ophthalmic* branch penetrates the orbit close to the similar branch of the fifth and runs along its side to the cutaneous sense organs on the snout. The *buccal* branch arises from the

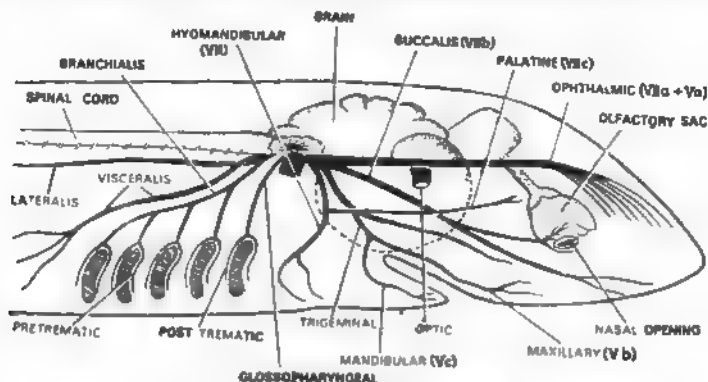


Fig. 3.54. Cranial nerves of the dogfish.

main root and runs along the maxillary and mandibular on the floor of the orbit. The *palatine* branch is a slender nerve which crosses the floor of the orbit. The *hyomandibular* branch which lies in the posterior wall of the orbit and passes in the direction of the spiracle. Looping around the spiracle the main ramus of the nerve continues closely beneath the skin to the lower jaw as the external mandibular branch and another branch runs down the hyoid arch as the *hyoidean*. The ninth or *glossopharyngeal* nerve arises from the medulla oblongata closely behind the eighth and innervates first gill-cleft over which it divides into a *pre-trematic* branch and a *post-trematic*, the former passing up and the latter passing down the first branchial arch. The *vagus* arises from the side of the medulla oblongata behind the ninth by a series of rootlets. The nerve has three main branches. The *lateralis* branch is quite prominent and long and runs posteriorly supplying the lateral-line receptor organs of the trunk. The *visceralis* branch continues backwards into the body cavity where it gives off branches to the heart and viscera. The *branchialis* branches into four subsidiary nerves supplying second to the fifth gill-slits, each nerve dividing into a pre- and a post-trematic branch, the latter running right down the gill-arch.

Spinal Cord. The spinal cord is of the typical vertebrate type. Beginning from the medulla oblongata it extends up to the end of the tail. There is a shallow *dorsal fissure*, a well marked *ventral fissure* externally and internally there is the *central canal* surrounded by grey matter consisting chiefly of *neurones*. Outside the grey matter lies the *white matter* comprising a non-nervous material made up of spider-like *neuroglia* cells and medullated nerve fibres.

Spinal nerves. From the spinal cord arise paired *metameric spinal nerves* at regular intervals along its entire length. Each spinal nerve arises by two roots a *dorsal sensory root* and a *ventral motor root* both uniting outside to form a definitive spinal nerve. The ventral root passes through a foramen in the cartilaginous neural arch of the corresponding vertebra. The dorsal root always arises in front of the ventral and bears a slight enlargement, the *ganglion*. Both run backward for a short distance then pierce the neural arch separately. The passage of the dorsal root is usually in the intercalary plate.

In the region of the pectoral fin the third, fourth, fifth and sixth spinal nerves run posteriorly and ventrally and then join each other by cross-connections forming the *cervicobrachial plexus* which gives off branches to the fin. One branch goes to the muscles of the body wall, and the other to the fin. The pelvic fins are supplied by ninth or tenth spinal nerves the posterior ones of which form the *lumbo-sacral plexus*.

Between the first spinal nerve and the vagus two or three small fibres arise from the medulla oblongata and unite to form the *occipital nerve*. A branch of the occipital nerve unites with the first two spinal nerves to form a *hypobranchial nerve*, which crosses the *branchiovisceral* branch of the vagus and turns ventrally to supply muscles in the floor of the mouth. It is likely that this nerve is homologous with the twelfth cranial nerve (*hypoglossal*) of higher vertebrates.

The *sympathetic system* is poorly developed in the dogfish and its constituent parts are difficult to find. According to available information it consists of a paired chain of lateral ganglia situated immediately above the peritoneum on each side of the middorsal line in close relation to the dorsal aorta. The first ganglion of these, situated behind the branchial plexus, is fairly large as it is formed by the fusion of several ganglia. It gives off branches to the viscera and is connected to numerous fibres from the spinal nerves. Several irregularly scattered ganglia are also met with. They send small branches to the kidneys and genital organs. The ganglia are in close association with *chromaffin bodies* on the anterior side.

The dogfish has no air-bladder. It is heavier than water (its specific gravity is 1.06 and that of sea-water is 1.03). It may sink in water while at rest, while in movement lift forces must be developed to keep it up. But the dogfish does not sink because the pectoral fins and the lower lobe of the tail mechanically keep the animal up. No nervous mechanism is associated with this.

All bony fishes possess the power of swimming backwards with the help of their very mobile fins and lamprey and eels can wriggle backwards by passing waves of muscular contraction forward from the tail to the head. This backward swimming mechanism appears to depend on the use of giant fibres in the spinal cord which transmit impulses directly from the motor centres of the brain to the hind end of the body. Such centres and fibres (the Müller fibres of the lamprey) are absent in sharks which cannot swim backwards. They always retreat by turning round and swimming back.

Sense Organs. The dogfish is an active free-swimming predatory organism as such it possesses an elaborate sensory system for guiding and controlling its movements. All the three primary sense organs, eye, ear and nose are well developed. In addition to these there are the lateral-line organs and the *ampullae of Lorenzini*, the functions of which seem to be associated with the aquatic mode of life.

Ampullae of Lorenzini. Over the surface of the head numerous small pores are scattered in definite groups. These represent the openings of the *ampullae of Lorenzini*. Each pore is connected with a mucous filled canal, the terminal portion of which is enlarged to form the *ampulla* or *ampullary sac* composed of dilated chambers supplied by delicate nerve strands coming from branches of the facial nerve. There are about eight or nine radially dilated chambers in each ampullary sac. They are separated from one another by septa and are arranged around a central core, the *canstrum*

(Fig. 3.54). Usually the ampullae are named according to their location on the head. Those lying above the supra-orbital canal are called **supra-opthalmic**, those lying between the supraorbital and infra-orbital canal are called **outer buccal** and those beneath the infra-orbital canal are called the **inner buccal ampullae**. These sense organs have been associated with the perception of pressure and of vibrations in water. But Sand (1938) has reported that such speculations are unwarranted and, on the basis of experimental work, he has assigned a **thermosensory** work to them.

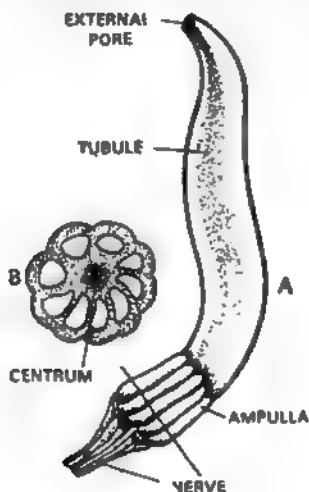


Fig. 3.55. Ampulla of Lorenzini of the dogfish. A, entire; B, cross-section of the ampullary sac.

Lateral-line System. The lateral-line system consists of a number of canals lying in the dermis. They open on the surface by numerous pores. Sensory receptors called **neuromasts** are located in the canals. The neuromasts are innervated by the branches of the seventh nerve and the lateralis branch of the vagus. The lateral-line proper extends from head to tail and lies over the lateral septum which separates the epaxial and hypaxial muscles of the body wall. On reaching the head each canal bends dorsally and is connected by its fellow of the opposite side by a transverse commissure the **occipital canal** (supratemporal canal), lying immediately behind the openings of the endolymphatic ducts. In front of this commissure each lateral-line canal, (cephalic canal) bends a little outward and forms the post-orbital canal. On reaching the posterior margin of the orbit it divides into a **supraorbital** and an **infra-orbital canal**. The supraorbital (Fig. 3.56) canal runs forward dorsal to the eye, the infraorbital canal lies between the eye and the spiracle and runs forward below the eye. The supra-orbital canal divides into two branches: (i) the dorsal branch running up to the tip of the snout and bending sharply backwards as the **ventro-lateral branch** running along the ventro-lateral edge of the snout, (ii) the anterior branch that bends downwards just in front of the eye and joins the infraorbital canal. At the junction of the infra-orbital canal with the ventrolateral branch of the supraorbital arises the **jugal canal**, just in front of the eye. It runs backward parallel to and beneath the infra-orbital canal. The **mandibular canal** arises from the jugal canal, at the angle of the jaws, and runs along the lower jaws right up to the lip.

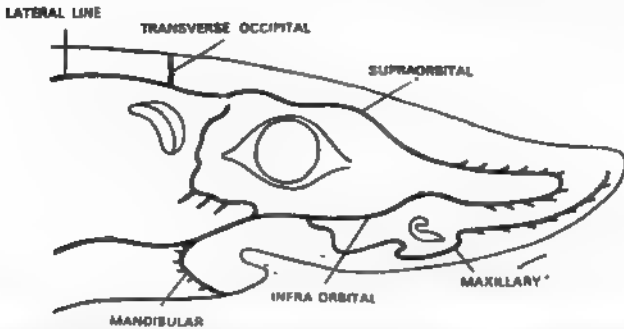


Fig. 3.56. Lateral view of the head of the dogfish showing the position of the canals of the lateral-line system.

The lateral-line system is an extremely sensitive and accurate method of locating objects such as other fish in the neighbourhood. Pumphrey (1951) points out that a group of vibration receptors will respond to a distant vibration according to their distance from the source of 'sound'. If the receptors are spread over a considerable length of the body and send impulses to a common centre the apparatus will become an efficient structure. This precisely is the nature of the lateral-line system which extends over the whole body and is innervated by cranial nerves from a single centre in the medulla.

The receptors of the lateral-line system are stimulated by slow vibrations of the watery environments and control the orientation of the body in relation to waves and currents (rheoreceptors). A shark whose sensations of sight and hearing are destroyed responds to wave-movements produced by throwing a stone into the water, but when the lateral-line nerves are cut no response to these vibrations occurs. The lateral-line system enables the animals to detect even the slightest disturbance in the surrounding medium even when the fish is in complete darkness of the ocean.

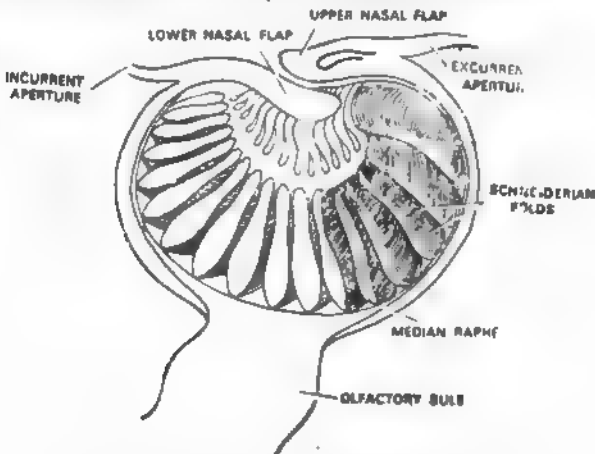


Fig. 3.57. Sagittal section through the olfactory organ of the dogfish.

Pit-organs. The pit-organs consist of ectodermal receptors located in pits, beneath which lie groups of receptor cells innervated by the nerve fibre. The pit-organs are found in large numbers in rays among elasmobranchs.

Olfactory Apparatus. Each naris on the ventral side of the snout opens into a blind olfactory sac. Each sac is formed as an ectodermal invagination, but does not communicate with the buccal cavity. It is relatively large ellipsoid sac, the mucous membrane of which is thrown into a double series of folds, the **Schneiderian folds**. There is a large number of these closely set folds, held in place by a median band of connective tissue, the **median raphe** (Fig. 3.57). The folds are lined by **olfactory receptors** intermixed with stiff supporting cells. The olfactory receptors receive fibres from the olfactory nerve. Externally a thin membrane covers each sac, lodged in the cartilaginous olfactory capsule on each side of the skull.

Each external naris is more or less completely divided into two, a **lateral incurrent siphon** and a **median excurrent siphon** by three nasal flaps. Of these flaps two project inward fitting closely one above the other; while the third hangs down from the dorsal side slightly overlapping the other two.

The median raphe of the Schneiderian folds lies parallel to the long axis of the nasal aperture, with the result that the current of water that enters through the incurrent canal is at first directed against the oral wall of the olfactory sac, then turns internally to the nasal valve in the direction of the median raphe and finally passes out through the excurrent siphon. The water thus enters at the lateral end of the nasal aperture and takes a zig-zag course through the olfactory sac finally leaving by the mesial end of the nasal aperture.

The olfactory sense is very highly developed in all cartilaginous fishes and is correlated with a highly developed sense of smell that enables them to detect food. If the external narial openings are plugged the dogfish will swim over food material without detecting it, and with one naris open it will detect even concealed food. The forebrain of these fishes is only a relay-station for olfactory impulses, not a structure dealing with learned behaviour.

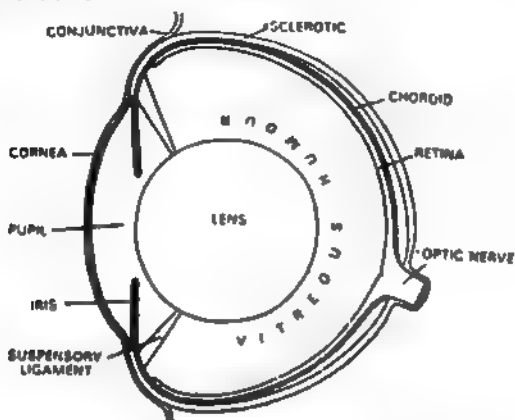


Fig. 3.58. Sagittal section through the eye of an elasmobranch.

Eye. The eyeball is almost hemispherical in shape. Only its outer surface is flat. It is held in position by six eye-muscles, and a cartilaginous stalk, the **optic pedicle**. The stout optic nerve may also be seen crossing the orbit and entering the eyeball. The eyeball consists of three concentric layers. The **sclerotic** forms the outer protective layer, opaque and cartilaginous in nature, and becomes transparent in front forming the **cornea**. The **choroid** is the connective tissue coat, richly supplied with blood

vessels, lying next to the sclerotic. It is continued in front as a strongly pigmented iris, bearing a median vertical slit, the *pupil*, which is not sphinctered in fishes. The retina is the innermost layer and forms the sensitive part of the eye. It is made up of special nerve cells called rods and cones. The *crystalline lens* is a spherical structure closely attached to the posterior surface of the iris. It divides the inner space of the eye into two unequal chambers, each filled with a semi-fluid substance. Aqueous humour fills the anterior chamber and vitreous humour fills the posterior chamber. The lens is supported by suspensory ligament.

The eye of the dogfish, like the human eye, is normally focused for distant objects, and it has to be accommodated for near vision. This accommodation, however, is brought about by moving the lens away from the retina and not by changing its shape. The retina itself is largely, if not entirely composed of rods which means that the fish is adapted for life in relatively low light intensities and is colour blind. Another adaptation to vision in dim light is provided by the presence of a silvery layer of *tapetum*, below the light-sensitive cells of the retina. This layer reflects extra light on to the cells.

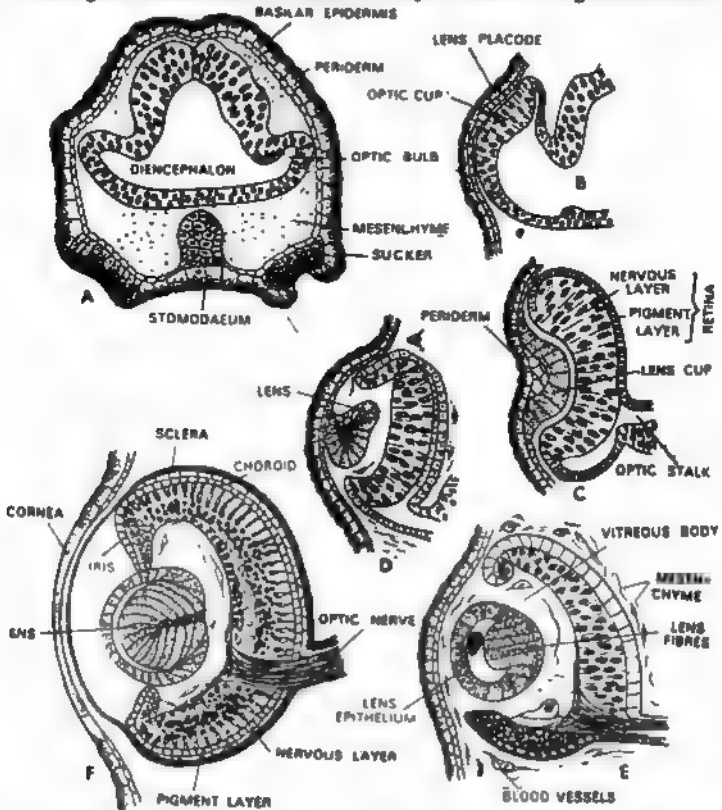


Fig. 3.59. Development of the eye in vertebrate. A, formation of optic bulbs, B, invagination of optic vesicle begins, C, rudiment of lens formed and it pushes into the optic vesicle (D); E, optic vesicle constricts forming iris and lens-vesicle separates; F, structure of embryonic eye, lens has become solid.

In some dogfishes this layer takes the form of a series of inclined planes which can be shuttered in strong light by a black pigment layer of contractile cells. In strong lights the iris also closes to an oblique slit. The two eyes are set wide apart as such they cannot be focussed together on any one point. Their fields of vision are separate. This arrangement has been called *monocular vision*, which is a rule in sharks. Another notable feature is that the lens can project through the pupil against the cornea therefore rays of light entering at a wide angle can be caught and focussed on the retina.

Development of the Eye. The tissue of which an adult eye is made are derived from three sources, the brain, the mesenchyme of the head and the embryonic epidermis. Early in the development, as the medullary groove is closed into a tube, an outpushing appears on each side of the ventrolateral parts of the fore-brain. Each of these soon differentiates into an enlarged distal portion the *optic vesicle* (or bulb) and a constricted proximal portion called the *optic stalk* (Fig. 3.59 B) that connects the vesicle with the brain. Meanwhile a patch of epidermis on the side of the embryo immediately opposite each optic vesicle has been thickening to form the rudiment of the lens. Next the terminal part of the optic vesicle invaginates (Fig. 3.59 C, D) to form a two-layered optic cup with its concavity towards the growing rudiment of the lens. The part of the optic vesicle that has not invaginated retains its epithelial character and forms the *pigment layer* of the retina, while the inner layer of the cup (invaginated part of the optic vesicle) becomes the *nervous layer* of the retina. The deeper cells of this layer differentiate into rods and cones while the more superficial cells form the nervous layer. Because of invaginations the cavity of the optic vesicle disappears and the two layers of the retina come to lie in contact with each other. They are, however, continuous at the rim of the cup.

Next the lens rudiment invaginates (Fig. 3.59 D), forms a hollow vesicle sinking towards the optic cup, and eventually separates from the outside ectoderm. The cavity within the embryonic lens is gradually obliterated by the columnar growth of cells that finally form mass of transparent refractive fibres, arranged chiefly in a meridional fashion (Fig. 3.59 F.). As the lens comes to lie in the cavity of the optic cup its rim constricts and persists as the *retinal pigment layer* of the iris, whereas, the openings of the optic cup persists as the *pupil*. The epidermis that is left after the separation of the lens forms the *conjunctiva*, which becomes transparent.

As the embryonic double cup appears, a deep notch, the *choroid fissure*, appears on its ventral wall. This extends up to the rim of the cup distally and proximally it continues as ventral groove on the optic stalk up to the wall of the brain. Eventually certain of the retinal neurons send out neurites, which after passing through the choroid fissure, run along the groove in the optic stalk and into the brain. These neurites form the *optic nerve*, while the optic stalk fades in importance and vanishes. The cells on the sides of the choroid fissure grow over the optic nerve finally closing the

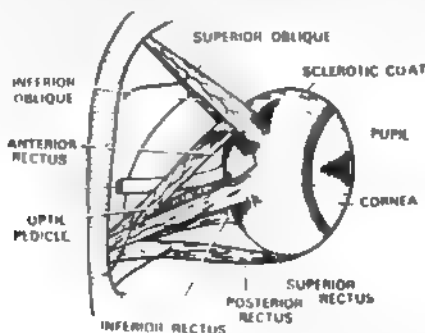


Fig. 3.60. Diagrammatic sketch showing the muscles of the eyeball.

fissure. Because of this the optic nerve appears to penetrate directly through the walls of the eyeball.

Muscles of the eye. The eye muscles consist of six narrow muscular bands which arise from the wall of the skull and are inserted into the eyeball. The recti muscles are four in number arising from the posterior end of the orbit (Fig. 3.63). The **superior rectus** runs outwards and upwards and is inserted on the dorsal surface of the eyeball. The **inferior rectus** runs outwards and downwards to be inserted on the ventral surface of the eyeball. The **anterior rectus** runs forward and is inserted on the anterior surface. The **posterior rectus** runs backward and is inserted on the posterior surface. The **oblique muscles** are two and arise from the anterior angle of the orbit close together. The **superior oblique** is inserted on the dorsal surface of the orbit in front of the superior rectus. The **inferior oblique** is inserted on the ventral surface of the eyeball.

The oculomotor or the third cranial nerve enters the orbit and divides into branches that supply the anterior rectus, the superior rectus, the inferior rectus muscles as well as the inferior oblique muscle of the eyeball. The trochlear or the fourth cranial nerve arises from the dorsolateral surface of the mesencephalon, and on entering the orbit supplies exclusively the superior oblique muscle of the eyeball. The abducens or the sixth nerve is a slender nerve arising from the medulla oblongata, and innervating the posterior rectus muscle on entering the orbit.

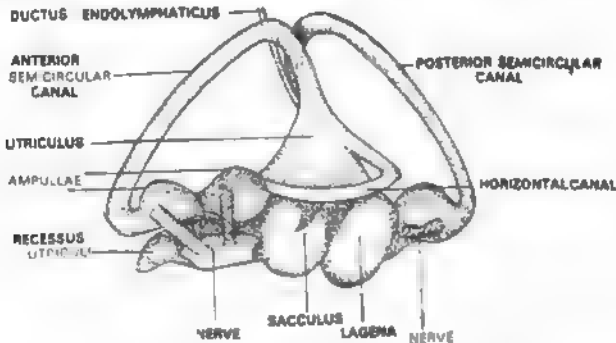


Fig. 3.61. Membranous labyrinth of the ear of the dogfish.

Ear. The ear or the stato-acoustic organ of each side is a closed ectodermal sac, the **membranous labyrinth**, which is enclosed within the cartilaginous auditory capsule. The interior of the membranous labyrinth is filled with a fluid known as **endolymph** containing a number of calcareous bodies called the **otoliths**. The membranous labyrinth consists of a central portion, the **vestibule**, and three **semicircular canals**. The vestibule (Fig. 3.64) is a laterally compressed sac differentiated by a constriction into a dorsal chamber, the **utricle** and a lower chamber, the **sacculus**, the posterior end of which forms an outgrowth, the **lagena**. From the sacculus arises a narrow tube, the **ductus endolymphaticus** which runs upwards and pierces the cranium. The semicircular canals are three tubular loops opening into the utricle. These canals are mutually at right angles, one being horizontal, the **horizontal canal**, and the other two vertical, the **anterior vertical canal** and the **posterior vertical canal**. The three canals are arranged in the three planes of space. At one end where it joins the utricle each semicircular canal is swollen out to form an **ampulla** (Fig. 3.64). The inner ear is innervated by the **auditory nerves** and is surrounded by a fluid, the **perilymph**.

Most of the ear in fishes is not concerned with hearing but stabilizes the eye movements when the body of the fish rolls and turns, thus keeping the visual field constant. Independent voluntary movements of the eye do not occur. It is probable that a small patch of sensory hairs in the utricle is responsible for true hearing. The main centre for the reception of low frequency vibrations is the lateral line system.

Another function, associated with the ear is to maintain equilibrium in space (or balance).

Development. In all vertebrates the auditory apparatus arises as a thickening, the **auditory placode**, of ectoderm on each side of the head of the embryo in the region of the hind-brain. The placode first forms a depression, the **auditory pit** (Fig. 3.62), and then sinks in as a hollow vesicle, the **auditory vesicle**, connected with the exterior by a pore. As the development proceeds this tube, embedded in the mesoderm, becomes longer and longer and in dogfish and some other types it forms **ductus endolymphaticus**. In other animals the ductus endolymphaticus, on the other hand, arises as an outgrowth from the auditory vesicle, after it separates off completely from the superficial ectoderm. From the innermost end arises the membranous labyrinth. The end enlarges to form the vesicle, which constricts giving rise to utricle and sacculus and finally the canals arise. Each canal rudiment is at first delimited by two parallel grooves, which deepen and then grow towards each other. Finally the grooves meet forming a septum that separates off a tubular canal from the utricular cavity. This tube lengthens and becomes curved forming a semicircular canal.

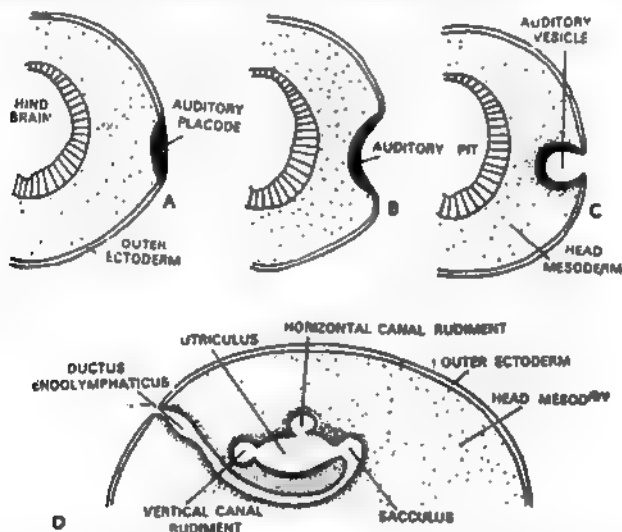


Fig. 3.62. Transverse section through the hind-brain region showing the development of the inner ear

The lower cyclostomes have the most abnormal ear that has a single canal flattened on the bottom and rounded dorsally. It bears ampullae at both ends. The lamprey (*Petromyzon*) and its relatives have paired canals which are dorso-ventral in position. The tube is lined by the epithelial cells with sensory processes, and the movement of fluid stimulates the cells and indicates body position. These animals cannot sense a three-dimensional world. This condition of cyclostomes is degenerate rather than primitive. It is so because of the semi-attached habit of these parasitic animals. In the elasmobranchs a third horizontal canal is added to the two dorso-ventral canals and each canal develops an ampulla at one entrance into the utricle. The semicircular canals are provided with crystals or concretions of calcium salts (otocysts) or otoliths (larger and more solid crystals). These organs in fishes are only static in function and have to do with the maintenance of equilibrium. On the posterior side the sacculus

develops a small out-pocketing, the *lagena*, in which there is a sensory area, the *macula lagena*, of doubtful function.

Endocrine System. In addition to the system of nervous co-ordination there exists another system of chemical co-ordination that is known as the *endocrine system* (Chapter 8). In *Scoliodon* only some of these glands have been located. Of these the *thyroid* and *thymus* are worth mentioning. The thyroid is an irregular mass of glandular tissues surrounded by a capsule of connective tissue lying just behind the symphysis of the lower jaw, ventral to the basihyal cartilage. The thymus appears in the embryo as a series of nodules, connected into a chain above the gill-pouches, but it disappears in the adult. The pancreas, the gonads, the pineal body, the pituitary gland, etc. have been seen in the dogfish but their endocrine physiology is not understood. An interesting account of the morphology of the adrenal complex is also available relative to other dogfishes, but nothing is known so far about the functions of the endocrine organs.

RENAL AND REPRODUCTIVE SYSTEMS

As in other vertebrates, the organs of reproduction and those for the elimination of nitrogenous waste in dogfish are closely related to each other. For this reason they are considered together.

Male. The kidney of the dogfish is *mesonephric*. Each kidney is a long, strap-shaped glandular structure lying against the dorsal body wall dorsal to the peritoneum, on either side of the median line. The kidneys extend through the entire length of the body cavity—from the root of the liver in front to the side of the cloaca behind. Each kidney is made up of an anterior slender portion the *genital kidneys* (*cranial mesonephros*) and a posterior thicker *renal mesonephros* (*caudal mesonephros*). The posterior portion is the functional excretory organ of the adult dogfish. The anterior portion, on the other hand, is almost without excretory tubules and extends forward to the front end of the body cavity beneath the peritoneum. The substance of the kidney is made up of coiled glandular uriniferous tubules each comprising a *Bowman's capsule* enclosing the *glomerulus*, and a coiled *renal tubule*, many of which open into a common *collecting tubule*, that leads posteriorly and the two empty through a single *urogenital papilla*, dorsally located in the cloaca.

Development. Each uriniferous tubule develops from a special mass of mesoderm that lies between the dorsal somite and the ventral unsegmented lateral plate (Fig. 3.63). This is the *nephrotome* the cavity of which is called *nephrocoel*. Internally the nephrocoel communicates with dorsal myocoel and the ventral splanchnocoel. Soon the nephrocoel becomes cut off from the somite above but its connection with the body cavity persists as the *peritoneal funnel*. Meanwhile from the lateral wall of the

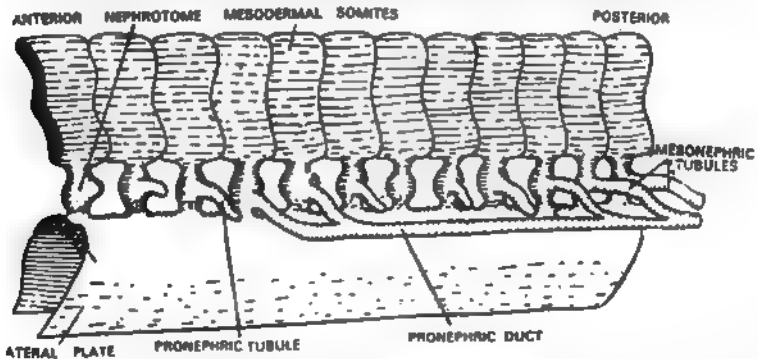


Fig. 3.63. Development of pro- and mesonephric tubules (after Goodrich).

nephrotome arise a diverticulum that grows out towards the ectoderm forming the glandular tubule ultimately. The diverticula are blind at first, elongate, bend backwards and fuse at their distal ends to form the **longitudinal duct**, which grows freely backwards, between the ectoderm and somatic wall of the coelom, and extends up to the embryonic cloaca.

The tubules develop first on the anterior segments of the body and continue growing backwards. Those of the more anterior segments, evidently develop early and become functional in the early life. Those of the later segments develop and function in later life, by which time the first formed tubules degenerate more or less completely. The

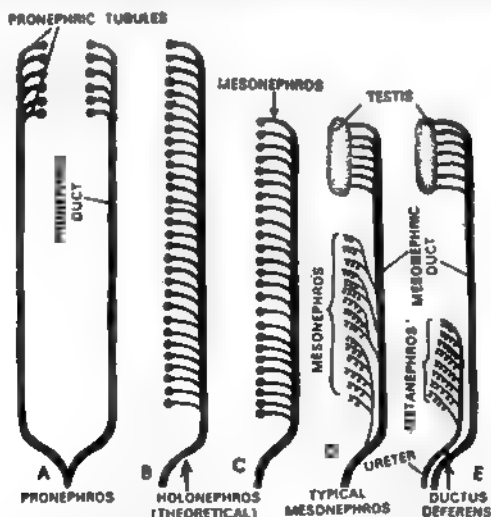


Fig. 3.64. Diagrammatic sketches of different types of kidneys.

kidney tubules formed in the first phase are known to form the **pronephros** or head kidney (because formed near the head). The tubules that appear later in the more posterior segments and take up excretory work later are known to form the **mesonephros**. The longitudinal duct of both the pro- and mesonephros is common. Further in the Amniota this second set of tubules (the mesonephros) is succeeded by yet more posterior set of tubules which make up the adult kidney or **metanephros**.

In the ancestral craniates, it is presumed, all the trunk segments were provided with paired tubules opening into a longitudinal duct. These tubules have been called **archinephros** (or **holonephros**) and their longitudinal duct leading to the cloaca the **archinephric duct** by some authors. Such an ideally constituted archinephros does not occur in the modern vertebrates except in the larval hagfish. Here the kidney consists of a single nephric tubule in each trunk segment opening on each side into a longitudinal duct draining to the exterior.

Pronephros. So far as the development is concerned the first kidney tubules formed in the anterior body segments constitute the **pronephros**, which is also the first kidney phylogenetically speaking. It is formed in the anterior end of the body and consists of 3-15 pairs of segmental tubules opening into the body cavity and connected with a longitudinal **pronephric duct**¹. In the primitive condition, it is presumed, each kidney

¹It is called by various names. It is archinephric duct being primitive; Wolffin duct after its discoverer and pro- and mesonephric ducts are names given to it on embryological ground. When serving as a kidney duct in the adults of lower vertebrate it is usually called ureter, but that is incorrect. When taken over by the genital system it becomes the duct of the epididymus and the ductus deferens.

tubule opened directly to the outside, therefore, the elimination of liquid waste by a common longitudinal duct may be considered a secondary measure. The pronephros functions in few adult vertebrate (amniotes and Chondrichthyes) in which it is exceedingly short-lived in the embryonic phase but it appears to function in the early developmental stages of those craniates which have little yolk in the egg and have a prolonged larval period. Usually the pronephric tubules do not have individual glomeruli but a single larger glomerulus (Fig. 3.65) that projects into the coelom in the neighbourhood of the nephrostomes of the pronephric tubules. Wastes excreted in the body cavity find their way into the pronephros and rally to the cloaca. In some cases (cyclostomes and bony fishes) the nephric part (the part in which nephric tubules lie) of the coelom is cut off from the coelom proper forming a separate pronephric chamber. The glomerulus of the pronephros is formed by the blood vessels of the gill-region and not of the kidney region, hence it is said to belong to the gills and not to the urinary system. This suggestion is quite consistent with the fact that the gills of fishes supplement the kidneys as excretory organs. The larval head kidney disappears in the adult amphibians and in many fishes. In many teleosts and hagfishes it remains functional throughout life although in other teleosts it is commonly modified into a mass of lymphoid tissue.

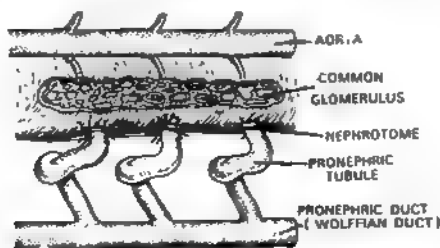


Fig. 3.65. Pronephric type of kidney showing a separate pronephric chamber.

The kidney of the dogfish presents a number of interesting morphological and physiological studies. The blood of the dogfish contains over two per cent of urea (typical excretory product of many higher vertebrates). The enzyme *arginase* responsible for the production of urea is present in large amounts in all the body tissues except blood and brain (Smith, 1936). Urea does not escape through the gills, and the kidney possesses a special mechanism for pumping it back into the blood almost as fast as it leaks out through the glomerular filter. This probably developed when the ancestors of the sharks migrated from fresh water into the sea. This means that the osmotic pressure of the blood in fresh water was much less than that of the sea water. Now the blood would lose water osmotically to the sea water, but this was prevented by getting urea back into the blood. This results in the increase of osmotic pressure in the interior and the balance is struck by a slight inflow of water from the surroundings, which can be dealt with by the kidney. The tissues of the body have become habituated to urea so much so that the heart will not beat in a physiological solution which does not contain urea, and the egg case is provided with a store of urea when it is laid.

In modern bony fish this mechanism of pumping urea back does not exist. They deal with the same problem (of raising osmotic pressure inside) by drinking sea water and excreting chloride through the gills. Blood urea is, however, present in the living freshwater lungfish, where it is brought into action during the dry season when the fish activates in the mud cocoon.

The testes (Fig. 3.66) are elongated extending more than half way backwards from the front end of the coelom and covered by peritoneum. The peritoneum suspending the testis in the body cavity is called the mesorchium. The Wolffian duct is well developed and is thrown into an intricate series of coils overlying the genital portion of

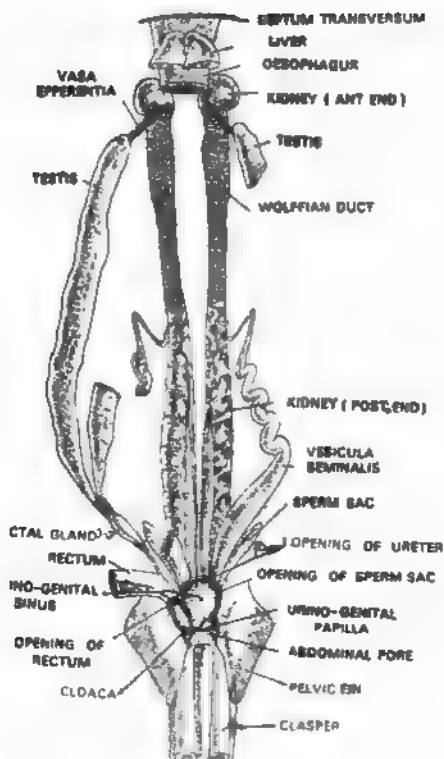


Fig. 3.64. Urinogenital system of the male dogfish.

the kidney and forming the *vas deferens* on each side (Fig. 3.66). The *vasa efferentia* are minute tubules which open into the anterior end of the *vas deferens*. The *vasa deferentia* become enlarged forming the *seminal vesicles*, on each side before they open into a large triangular chamber, the *urinogenital sinus*, which finally opens into the cloaca on an elevated *urinogenital papilla*. The *sperm sacs* (Fig. 3.66) are two blind elongated outgrowths of the *urinogenital sinus*, whose function seems obscure. During copulation the sperms from the cloaca pass into the claspers which are inserted into the cloaca of the female. The *claspers* are grooved elongations of the pelvic fins which are inserted into the cloaca of the female during copulation. The sperms from the cloaca pass into claspers and are transferred to the female through them. There are certain muscular sacs called *siphons* lying beneath the skin of the ventral surface in the pelvic region. Posteriorly these sacs extend as *siphon tubes*, each of which opens into the groove of the clasper of its side. The use of the siphons seems to be obscure, though it has been ascribed the function of flushing spermatozoa accumulated in the claspers into the female cloaca by squirting out the contained sea water.

Female. The kidneys are paired, each showing the differentiations into an anterior and posterior portion. The ureters commence in the anterior part and continue backwards, and in the region of the functional kidney each dilates and joins its fellow of the opposite side forming a common duct opening into the urinary sinus, a

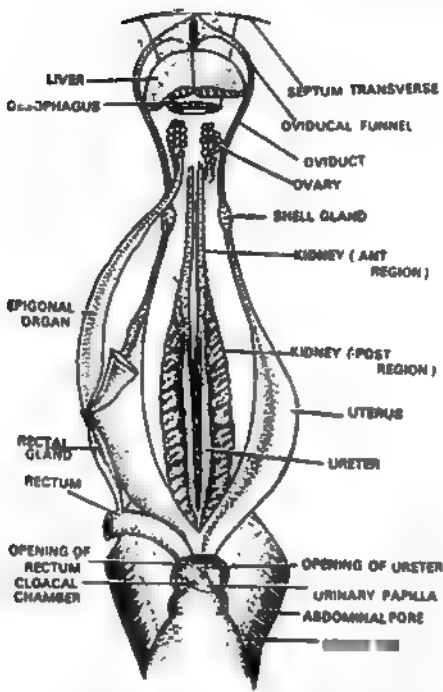


Fig. 3.67. Urinogenital system of the female dogfish.

triangular chamber. The sinus opens into the cloaca at the tip of the urinary papilla.

The ovaries (Fig. 3.67) are paired¹ organs varying in size and form according to the age. In the mature female they are lobulated due to the presence of large eggs in the interior. They lie on either side of the vertebral column suspended in the body cavity by folds of peritoneum, the *mesovaria*. The *epigonal organ*, a long tubular strand of tissue of unknown function, extends between the ovary in front and the caecal glands behind. The *oviducts* are the well-developed *Müllerian ducts*, each of which is a stout tube. The anterior coelomic opening of these have coalesced to form a single wide longitudinal aperture, the *oviducal funnel* (or *ostium tubae*). From the common aperture each oviduct narrows slightly and passes backwards at the sides of the coelom to the cloaca. At about one-third of the way down its anterior end each oviduct swells out to form the *oviducal gland* or *shell gland* which is responsible for the secretion of the egg case. Behind the glands the oviducts are large and dilatable with longitudinally folded walls. Posteriorly they unite and open by a large median aperture into the dorsal wall of the cloaca. Before uniting each oviduct suddenly enlarges forming very wide chambers called the *uteri*. In *Scoliodon* and other viviparous forms the uterus serves as a place for the development of the young. It contains a variable number of embryos in different species (7 in *Scoliodon sorrakowah*) and fills the greater part of the abdominal cavity. The mucous lining of the uterus becomes divided into as many compartments as there are embryos (Fig. 3.69). The two uteri unite to form a median

¹ In many dogfishes there is only a single large ovary

chamber, the **vagina**, which opens by a large aperture into the cloaca. A fold of mucous membrane between the vagina and cloaca acts as a valve and closes the **vagino-cloacal aperture**. The cloaca is a shallow depression between the pelvic fins. In the female there are three openings into it, the rectum in front, the genital aperture in the middle and the urinary sinus behind.

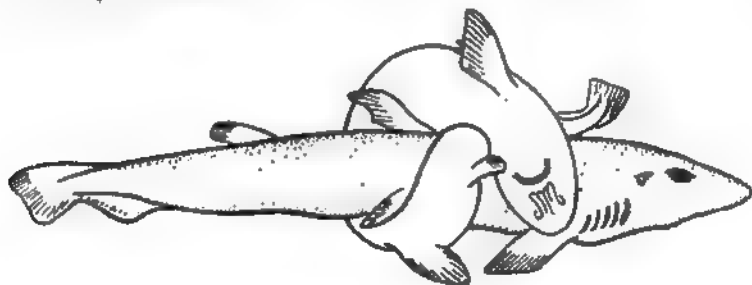


Fig. 3.68. Copulation in the dogfish.

All the elasmobranchs produce large yolky eggs, generally protected by a horny egg case, and internal fertilization is therefore necessary. In a few forms including *Scoliodon* the whole development takes place in the oviduct of the mother, a number of eggs sharing a common thin-walled egg capsule or compartment. Occasionally there is a placental attachment of the yolk sac to the uterine wall. In *Scoliodon sorrakowah* one uterus may contain as many as seven embryos but in *S. palasorrah* only three embryos have been reported from each uterus. The number seems to vary in different species.

Copulation. For the internal fertilization the claspers are inserted into the cloaca of the female. How this is brought about in the common dogfish was studied by Bolan as early as 1881. The male coils itself around the body of the female in a curious back-to-back position (Fig. 3.68). The method provides firm grip in the rough-skinned forms (*Scoliodon scyliorhinus*). It is likely that the dorsal fin spines of some species also aid pairing. (In the modern chimacrioid fishes a spiny head clasper is present probably aiding copulation).

Development. The ripe eggs are released into the body cavity by the rupture of the mature follicles. They are carried by the coelomic fluid to the anterior part of the coelom where they are picked up by ostium tubae. Passage down the right or left oviduct seems to be a matter of chance. Spermatozoa in the upper part of the oviduct fertilize the eggs as they pass down. Development of the embryo takes place in the uterus.¹

The fertilized eggs develop very slowly, 48-day old dogfish embryo is at almost the same stage as a 48-hour chick embryo. This difference is because of the different temperature of development. If the temperature of development of the dogfish is raised the rate of development is accelerated. Normally the time taken by the dogfish development is about 16 to 25 months. The development of elasmobranchs is by partial cleavage that produces a blastoderm, perched on the top of a large mass of yolk. As soon as this grows further it develops a tubular yolk-stalk connected at one end with the intestine of the embryo and at the other with a yolk-sac, filled with yolk for the nourishment of the developing embryo. In the later stages when the yolk is more or less used up the yolk-sac becomes folded and gets embedded in the wall of the uterus forming a yolk-sac placenta. Thus the embryo starts drawing its nourishment from the maternal tissue. As the placenta is formed blood vessels develop in the yolk stalk, which now becomes placental cord attached to the embryo in the midventral line at a point in level with the anterior edge of the pectoral fins. The placental cord is

¹ In *Squalus acanthias*, which is ovoviviparous a beautiful clear amber-coloured egg-case is formed around several eggs and the early development takes place within this shell or egg-case.

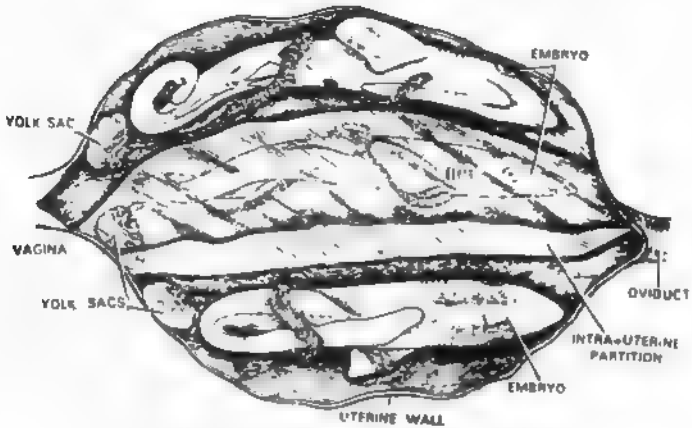


Fig. 3.69. Uterus of the dogfish cut open to show the embryos inside.

twisted round each embryo and ends in the folds of the yolk-sac placenta which is usually attached to the vaginal end of the uterus. Each placental cord is provided with numerous delicate tubular processes, the *appendicula*, each of which is made up of several layers of epithelial cells surrounding a central core of loose connective tissue. In *Scoliodon sorrakowah* the *appendicula* may be simple or forked, and the placenta is least modified. It is the original yolk-sac of the typical ovoid form. At its lower extremity it has a number of small protuberances, which are embedded in the uterine tissue of the mother. The function of the *appendicula* is probably the absorption of nutritive material secreted by the uterine wall of the mother. This conclusion is based on the fact that the *appendicula* are best developed in the species that have vestigial placenta.

The young dogfish which is produced when the egg hatches is just a miniature of the adult. Later life-history of the dogfish is not known. Attempts to catch recently hatched small dogfish "fingerlings" (very young fish) have not succeeded. It is not known where they spend the first year or so of their life. Since all the dogfish caught are of surprisingly uniform size and sexually mature, it seems as though the early life may be spent off-shore, the mature fish returning to shallow water perhaps for the purpose of breeding or egg laying.

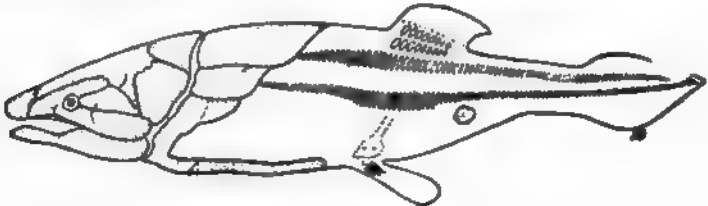


Fig. 3.70. The placoderm.

Relation to Man. The nuisance value of sharks is enormous, especially to the fishermen. They remove bait or fishes from hooks; steal netted fishes and often tear the nets. Some larger species even injure fishermen and often capsize small boats. In north temperate waters occasional human deaths have been reported due to injuries caused by

the spines of sting rays. *Carcharodon carcharias*, the great white shark, attacks human being in Australian waters.

Food value of sharks and rays is not much. They are used as food only in some countries. Along the Indian coasts only poor people consume them. In Ceylon, the Philippines and California fins of sharks are gathered and boiled to give rise to a gelatinous material that is favoured for soups. Skin of sharks tanned with scales, produces shagreen, which was used, in the old world, for casing fine books, jewel boxes, sword handles, etc. Shagreen is also used as an abrasive for polishing wood and ivory. The shark skin is also tanned with crushed scales giving rise to leather for shoes and bags. In Greenland, Iceland and Norway sharks are caught on a large scale in order to extract oil from their liver. A large basking shark yields 125 gallons of shark-liver oil. The oil, rich in vitamin A, is used, like cod-liver oil, by human beings.

Fossil Relations. The fossil history of the sharks is small. In fact the earliest known fossils of the animals with jaws are those included in the class Placodermi of Silurian and Permian time. They were provided with primitive jaws with unmodified hyoid preceded by a complete gill-slit (see below). The first elasmobranch has been obtained from the mid-Devonian rocks (some 300 million years ago) later than the first bony fishes, which also occur side by side. These were already well advanced in the evolution of jaws. No true bone is recognised in any of the sharks living or fossil and the cartilaginous skeleton seems more likely a degenerate rather than a primitive character. The Devonian shark *Cladoseleache* possessed enormous forwardly placed eyes, widely gaping jaws and powerful teeth all features suggesting that it was an active predatory form. The tail possessed a narrow root with lateral keels for streamlining in motion and its broad symmetrical scythe-like form indicates that the body was capable of high speed. The fossils of *Cladoseleache* are abundant because of large food availability. Some 200 million years ago in Permian and Triassic periods the sharks had a bad period, because the supply of bony fish that formed their main food ran short during this period. The successful sharks of this period developed crushing teeth and ventrally placed mouth suited for feeding on molluscs and similar bottom living forms. The Hybodonts with teeth and jaws of this type were the main marine forms of this period. But 120 million years ago in the Cretaceous times a new host of bony fishes invaded the sea from fresh water. They gave new lease of life to the surviving sharks that branched into two main line the flattened bottom feeding skates and rays that continued to feed on the bottom inhabiting molluscs, etc., and free-swimming active hunters represented by the modern sharks.



Fig. 3.71. Dogfish (gill-slits are seen below and behind the eyes).

CLASSIFICATION

The superclass Gnathostomata includes craniates in which one pair of the visceral arches is modified to form true paws. The nasal capsules or tubes are present. Internal ear with three semi-circular canals; and usually with paired appendages (fins or limbs). Sexes are separate. The superclass is divided into several classes including the Placodermi, Elasmobranchi, Teleostomi, Dipnoi, Amphibia, Reptilia, Aves and Mammals. Here the classification of only first two classes is given.

Class I. PLACODERMI (Aphetohyodea). Ancient fishes, Gnathostomes with primitive jaws in which the hyoid arch played no part in support of the jaws and the spiracle was, therefore, a typical gill-slit. The body covered by a heavy armour of bone comprising bony scales or plates (Fig. 3.70). The class has several orders. All are fossil

forms, none of which seems to have survived the Permian.

Chimatus (order Acanthodi) Silurian-Permian; **Coccoosteus* (order Arthrodira) Silurian-Devonian; **Lunaspis* (order Macropetalichthyida) Devonian; **Bothriolepis* (order Antiarchii) Devonian; etc.

Class II. ELASMOBRANCHII (Chondrichthyes). Cartilaginous fishes including sharks, rays and chimaeras. Fishes with cartilaginous endoskeleton, placoid scales cover the body, and abdominal pelvic fins provided with claspers in the male. The external opening of the cloaca serves as a common outlet for the rectum as well as the renal and reproductive ducts. Operculum is absent except in the Holocephali and the gills are laminar. There is a conus arteriosus, an optic chiasma and a spiral valve in the intestine. The oro-nasal groove, the pericardioperitoneal canal and the large sinuses in the venous system are the characteristic features of the class. The eggs are large and provided with a horny case. There is no air-bladder. With very few exceptions exclusively marine.

The class Elasmobranchii is divided into two sub-classes and many orders as follows.

Sub-class Selachii. The Elasmobranchii in which the pectoral fin has cartilaginous rods (propterygium, mesopterygium, metapterygium) supporting it. Fins are well developed. The caudal fin is heterocercal. This subclass has four orders in which only two have recent forms others are extinct.

***Order 1: Cladoselachii.** Extinct. Devonian to Permian. **Chadoseleache*, **Goonichia*.

***Order 2: Pleuracanthodii.** Extinct. Devonian to Trias. **Pleuracanthus*.

Order 3: Protoselachii. Devonian to Recent. **Hybodus* *Heterodontus*.

Order 4: Euselachii. Jurassic to Recent. This order includes most of the modern elasmobranch fishes. It is divided into two suborders.

Suborder 1: Pleuramata. Jurassic to Recent.

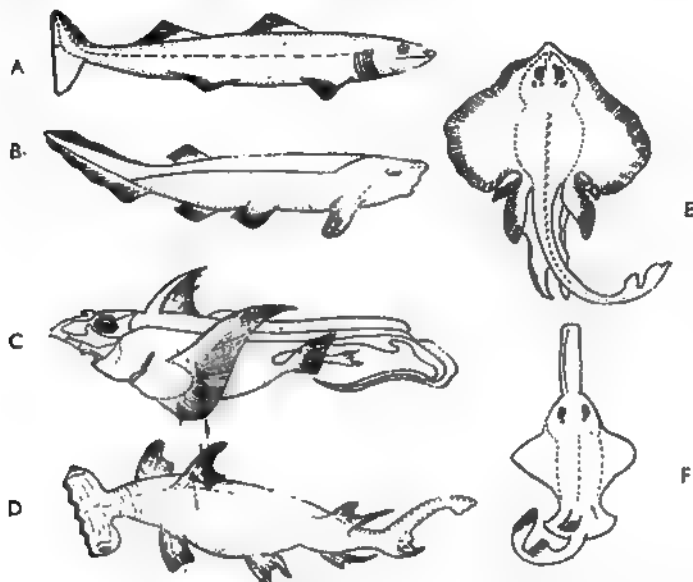


Fig. 3.72. Different types of cartilaginous fishes. A, Cladoselache; B, Hepatanchus; C, Chimaera; D, hammer-head shark; E, skate; F, sawfish.

Superfamily 1: Notidanoidea. Jurassic to Recent. *Hexanchus*.

Superfamily 2: Seyllioidea. Jurassic to Recent. *Scyliorhinus*, *Musletus*, *Cetobius*, etc.

Superfamily 3: Squaloidea. Two dorsal fins with spines; anal fin absent; gill openings 5-6, sixth gill-arch absent or complete; suspensorium hyostylic; rostral cartilage single; notochord constricted; vertebrae monospondylic; centra cyclo or tectospondylic.

Family Seyllidae. *Stegostoma*. Tiger-shark. With alternating brilliant dark brown and white bands over the body and fins. Attains a length of fifteen feet. Inhabits Indian Seas.

Family Carcharidae. *Zygacna*, hammer-headed shark. Head transversely expanded with eyes at the extremity of the head lobes; mouth ventral and crescentic; spiracle absent; viviparous. Temperate and Tropical Seas.

Bull-head sharks, whale-sharks, ray-like sharks, shark-sawfish (*Pristiphorus*), and *Squalus*, *Etmopterus*, *Somniosus*, *Pristiphorus*, *Alopias*.

Superfamily 4: Galeoidea. Two dorsal fins without spines; an anal fin; gill-openings 5, sixth arch rudimentary; suspensorium hyostylic; rostral cartilage triradiate; notochord restricted; vertebrae monospondylic.

Scoliodon (family Carcharinidae), *Loxodon*, *Carcharinus*; *Physdon*, *Galeus*, *Galeocerdo*; *Hemigaleus*, etc.

Superfamily 2: Hypotremata. Jurassic to Recent. Skates and Rays. Body flattened dorso-ventrally; pectoral fins enormously expanded anteroposteriorly, gill openings ventral five in number; spiracles present and dorsally placed behind the eyes; caudal region usually slender; dorsal fins, if present, on the tail, without anal fin (Fig. 3.72).

Example *Pristis* (family Pristidae). Saw-fish. Snout produced into a rostral process of cranium and provided with lateral saw-like teeth, body disc-like and gradually passing into the comparatively thick tail. Tropical and sub-tropical.

Example *Rhinobatus* (family Rhinobatidae). Guitar-fish. Tail long strong and without serrated caudal spine, rayed portion of pectoral fins not continued to the snout; electric organ absent, viviparous. Tropical and sub-tropical.

Example *Torpedo* (family Torpedinidae). With an electric organ between the pectoral fins and the head and occupying the whole space between the dorsal and ventral integument, and consisting of vertically arranged columns of prisms supported by walls of connective tissue and divided by horizontal septa of the same material into a number of compartments. A closer examination reveals that these are filled with gelatinous tissue through the middle of which runs a horizontal plate composed of a fine granular nucleated substance and of numerous nerve endings. These nerves are derived from four nerves which originate from an electric bulb of the medulla oblongata. Shocks from these can disable a man. Mediterranean, Atlantic and Indian Oceans.

Example *Raja* (family Rajidae). Skates. Disc broad and rhombic formed by pectoral fins extended on either side; caudal fin rudimentary, males with patches of claw-like retractile spines on the upper side of the pectoral fin. Seas of both hemispheres.

Example *Trygon* (family Trigonidae). Sting-rays. Tail long and slender and with long serrated spine. Temperate and tropical seas (Fig. 3.74).

Example *Myliobatis* (family Myliobatidae). Eagle-rays. Large pectoral fins which are not present at the side of the head but reappear at the extremity of the snout as a pair of detached fins; tail long, thin and whip-like; viviparous. Temperate and tropical seas.

Subclass 2. Bradyodonti. Devonian Recent

*Order 1. Eubradyodonti. Devonian to Permian.... Example **Helodus*.

Order 2. Holocephali. Jurassic to Recent.

Unique order having fishes with four gill-clefts covered over by an operculum, adult with naked skin, spiracle absent, skull autostylic, eyes large and high up on the head; mouth small, ventral and bounded by lip-like folds; three pairs of teeth in the form of tritural plates; nostrils confluent with the mouth; anterior dorsal fin has a strong spine on its front border; tail prolonged, in *Chimaera*, into a long filament; extra claspers on the head (the anterior clasper) and others in front of the normal abdominal pore;

notochord unsegmented and with numerous calcified rings in place of vertebrae; urinogenital part of the cloaca separate from the rectum. The upper jaw is immovably fused with the cranium not suspended by ligaments as in other elasmobranchs. Only three living genera occur. Of these *Chimaera* is quite well known and occurs on the Pacific coast of North America, Europe, Japan, Australia and in the Cape of Good Hope.

4. Class Teleostomi (Osteichthyes)

The Osteichthyes (G. *osteon*, bone + *ichthys*, fishes) form an important class including quite an extensive variety of fishes whose endoskeleton is primarily bony. The common name fish is derived from Latin *pisces*. They are aquatic vertebrates and possess the usual adaptation of gills for respiration, and paired fins as well as median fins to assist in locomotion. Various species inhabit all sorts of waters, fresh, brackish or salt, warm or cold. Fishes have been a staple protein food of mankind since antiquity and many species provide pleasant recreation of sports to fishermen.

The typical shape of the fish's body is fusiform or spindle-shaped with all the original features of streamlining. The skin is covered with dermal scales (ganoid, cycloid or ctenoid) and is provided with many mucous glands. Some fishes have scaleless or naked skin, and a few have enamel covered scales. The body is provided with both median and paired fins (with some exceptions only) supported by cartilaginous or bony fin-rays. The head bears usually a terminal mouth provided with well-developed jaws articulated to the skull. Two dorsal olfactory sacs are present (not connected to the mouth), eyes are large and devoid of eyelids. The endoskeleton is mainly bony, the sturgeons and some others with cartilaginous skeletons being exceptions. The vertebral column consists of many distinct vertebrae, usually with persistent relics of notochord. The tail, however, is homocercal. The heart is two chambered (one auricle and one ventricle) and is provided with a sinus venosus and a conus arteriosus, but it contains only venous blood (being single circuit heart). The red blood corpuscles are nucleated and oval. The respiratory organs are gills borne by bony gill-arches, located in common chamber at each side of the pharynx and covered by an operculum. They are also provided usually with air bladder sometimes with duct to the pharynx. The body temperature is variable depending upon the environment. Typically the gonads are paired. Usually these fishes are oviparous, but exceptional ovoviviparous and viviparous forms are also met with. With some exceptions, the fertilization is external. The eggs are minute and may be up to 12 mm. in diameter. The quantity of yolk differs with species. The segmentation is usually meroblastic and no embryonic membranes are formed. Sometimes the early young ones may be unlike the adults. The brain of the bony fishes shows definite structural advance. The ancient fishes had well-developed bony armour but the most modern fishes have less-developed bony armour. The size of these varies greatly. The smallest fish is a Philippine goby (*Paduka*) that is only 10 mm. long. The common length of the majority falls under three feet. Some recorded large specimens include nine-feet long halibut, the twelve-feet long sword fish, and the Columbia River sturgeon about twelve-and-a-half feet long weighing about 1,285 pounds.

TYPE LABEO ROHITA

The Indian carp, *Labeo rohita* (rohu) is one of the common bony fishes inhabiting fresh water throughout India and Burma except in Madras and Western Coast. The fish attains three feet or more in length and is dark or bluish black with a red mark on each scale. In some specimens the fins are black. Related species of the genus, *Labeo* are also found in tropical Africa, Syria and Malay Archipelago. *Labeo rohita* is esteemed excellent as food and is, therefore, propagated with care now all over the country.

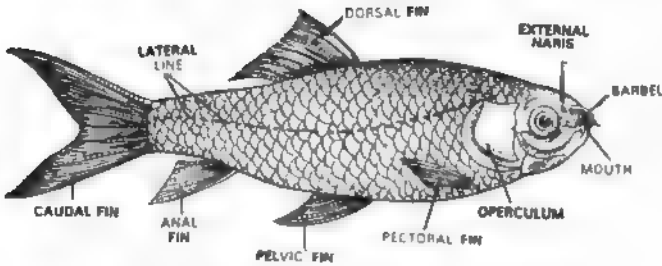


Fig. 4.1. External features of *Labee rohita* shown in a lateral view.

FORM OF BODY

The body is spindle-shaped moderately elongated, higher than wide, round or oval in cross section, for easy passage through water. It is divided into three portions, the head extending from the tip of the snout to the hind edge of the operculum, the trunk extending from this point to the anus, and the tail.

The head is about 4 to 5 inches long. Its dorsal profile is more convex than that of the abdomen and somewhat concave over the orbit. The snout is obtuse, depressed, scarcely swollen, but projecting beyond the jaws. The snout is devoid of lateral lobes, unlike other members of the genus. The mouth is inferior transverse opening, the edges of which are inclined backward making it crescentic. The mouth is bounded by thick fringed lips, with a distinct fold above and below (Fig. 4.2). The nostrils are double

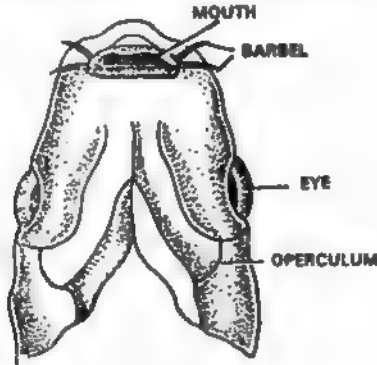


Fig. 4.2. Ventral view of the head showing the operculum and ventrally placed mouth surrounded by lips.

situated dorsally on the snout, a little in front of the eyes. These represent the openings of the olfactory sacs, each of which has two openings. The eyes are large, lateral and have no cycloids, but the cornea is covered by transparent layer of skin. There are generally two barbels located on the maxilla, hence called Maxillary barbels. They are relatively short and thin in this species. Sometimes another pair of barbels (costral pair) has also been reported in some species. The operculum or gill-cover is a large, thin flap on each side of the posterior region of the head. Between the operculum and

the side of the body is the large crescentic **gill-opening** from which the respiratory current makes its exit. Internally the operculum is supported by four thin bones, the outline of which can be made out through the skin. Under each operculum are four comb-like **gills** which can be seen by raising it.

The **trunk** is the region following the point where the operculum ends. It is covered by thin rounded dermal scales arranged in lengthwise and diagonal rows. There are six to six-and-a-half rows of scales between the lateral line and the base of the ventral fin. The free posterior edges of the scales overlap others like shingles on a roof (Figs. 4.1 and 4.3). Each scale lies in a dermal pocket and grows throughout life. The lateral line (Fig. 4.1 and 4.3) runs along either side of the body. Each is a row of small pores connected to a lengthwise tubular canal, under the scales, in which are located the sensory organs responsive to slow coarse vibrations in the water.

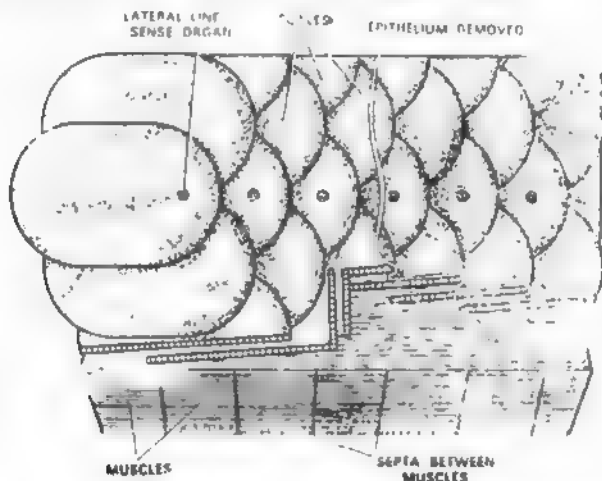


Fig. 4.3. Integument of a bony fish showing the arrangement of scales and underlying muscles.

The **dorsal fin** (Fig. 4.1) arises about midway between the snout and the base of the caudal fin. It is not quite so high as the body and its upper edge is moderately concave. The **caudal fin** is homocercal, i.e., it is a large vertically expanded structure deeply forked behind, the two lobes being symmetrical. It is supported by a number of flattened bony rods (hypurals) which lie on both the dorsal and ventral side of the urostyle. The caudal fin is the only organ of locomotion. Along with the myotomes it brings about movement of the body. Other fins are organs for balancing. The **anal fin** is on the ventral side inserted below the third or fourth dorsal ray. The **pectoral fins** are large, borne by the pectoral girdle, behind the opercula, and are as long as the head excluding the snout. The pelvic fins are supported by the pelvic girdles and lie close behind the pectorals. The anus and urinogenital aperture lie just in front of the anal fin.

Integument. The entire body of the fish is covered by soft mucous-producing **epidermis** (Fig. 4.3) that facilitates easy movement in the water and is a protection against entry of disease organisms. The integument of the trunk and tail is covered with cycloid scales. Below the integument lies the body wall musculature. The muscles of the trunk and tail are arranged in zigzag manner, as in the dogfish. There are special muscles to control the movement of fins, jaws, hyoid, operculum and branchial arches.

Coelom. The coelom is the cavity lodging the organs of the viscera. It is lined with

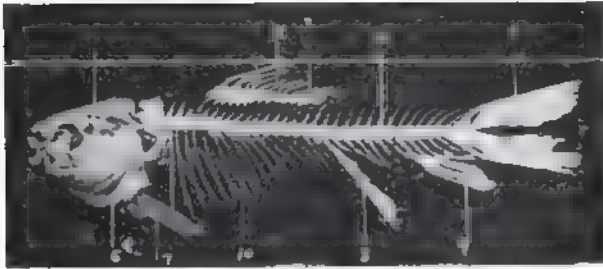


Fig. 4.4. Photograph of the skeleton of *Labee rohita*. 1, skull; 2, fin-rays; 3, dorsal fin; 4, vertebral column; 5, caudal fin; 6, pectoral girdle; 7, pectoral fin; 8, pelvic fin; 9, anal fin; 10, pleural ribs.

peritoneum and is divisible into a large abdomen containing the chief viscera and a small pericardial cavity containing the heart below the branchial arches.

ENDOSKELETON

The exoskeleton of the *rohu* consists of the scales and finrays, whereas, the endoskeleton comprises the vertebral column, ribs, skeleton of the median fins and the skull (axial skeleton) and the appendicular skeleton including the pectoral and pelvic girdles with the skeleton of respective fins.

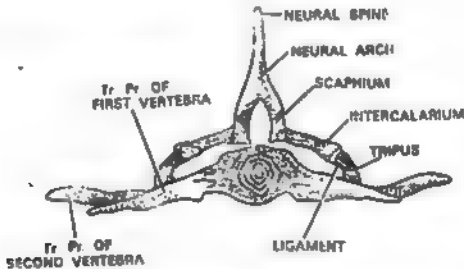


Fig. 4.5. Front view of the first trunk vertebra of *Labee rohita*.

Vertebral Column. The vertebral column consists of 37 to 38 completely ossified amphicoelous vertebrae grouped into two regions (a) the trunk vertebrae, and (b) the caudal vertebrae. There are twenty-one trunk vertebrae (Fig. 4.4), the typical of which are from the fifth to the twenty-first. The centrum is short, bony and concave at both the ends (hence amphicoelous). In the young stage the centrum is traversed by a narrow notochordal canal, lodging the notochord, which closes in the adult stage. The two contiguous vertebrae are connected by connective tissue and ligaments and the biconvex space between them is occupied by the remains of the notochord. The neural arch is formed by the fusion of the bony neurapophyses arising from the anterolateral borders of the dorsal surface of the centrum, where a large median dorsal depression is situated. Dorsally the neural arch is produced into a long backwardly directed neural spine. The base of the neural arch is thickened forming pre-zygapophyses, blunt processes directed upwards and forwards on the anterior side, and postzygapophyses, on the posterior face. These are directed upwards and backwards. These processes interlock the contiguous vertebrae and keep them in position. They are therefore

called the articular surfaces. Then occur a pair of short processes, the **parapophyses**, arising from the ventro-lateral surfaces of the centrum. To each of these a rib is attached. They are distinct and separate in the anterior thirteen or fourteen vertebrae except the first four. In the last three or four they are firmly fused with the anterior edges of the ventro-lateral depressions and pass outwards, backwards and downwards. These last vertebrae also have backwardly directed spine-like **postero-ventral processes** on the ventral side.

Weberian Ossicles. The first four vertebrae are without parapophyses and are modified to connect the air-bladder with the ear of fish (**Weberian ossicles**) and afford surfaces for the attachment of the constriction muscles of the pharyngeal bones. The fourth forms a basal and supports the **septum transversum**. The neural arch of the first vertebra consists of two small bony pieces, the **claustrum** and **scaphium**, the two anterior-most elements of the chain of bones called 'Weberian ossicles'. The other elements of the Weberian ossicles include the **intercalarium** and **tripus** (Fig. 4.5). The centra of the second and third vertebra are fused to form a single large centrum, the posterior half of which carries on each side a flattened triangular bone, the **tripus**, the posterior most element of the Weberian ossicles. A stout ligament stretches between the scaphium and tripus. On each side of the ligament is embedded a very small nodule, the **intercalarium**, with a short backwardly directed spine-like process. The tripus presses against the anterior wall of the bladder and the scaphium fits on the membrane covering a median posterior extension of the perilymph cavity of the ear.

Caudal Vertebrae. The tail region has seventeen vertebrae. In a typical caudal vertebra the **centrum** is biconcave, the **neural spine** is long and directed backwards and the articular facets are present on the usual places. Ventrally the centrum supports a **haemal arch** (Fig. 4.6) drawn out into a **haemal spine**. The bases of the haemal arches

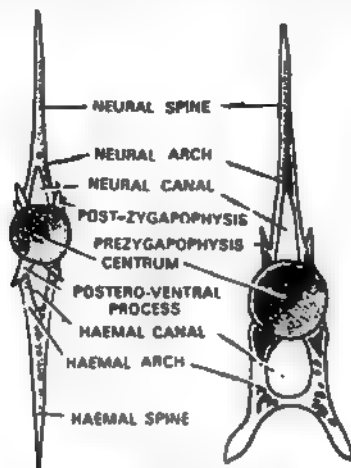


Fig. 4.6. A, posterior view of the caudal vertebra; B, anterior view of the first caudal vertebra of *Labeo*.

are thickened forming small blunt processes both anteriorly and posteriorly called **anteroventral** and **postero-ventral processes** respectively. The last three caudal vertebrae support the caudal fin, the last is turned upwards forming a rod-like **urostyle**.

The skeleton of the median fins comprises. (i) a series of parallel bony rods the **somactidia** or **radials**, and (ii) the **dermal fin rays** or **dermotrichia**. In *rohu* the **dermotrichia** are jointed, branched and have a bony texture (**lepidotrichia**); and besides these a second set of horny rays, the **actinotrichia**, persist at the free margins of

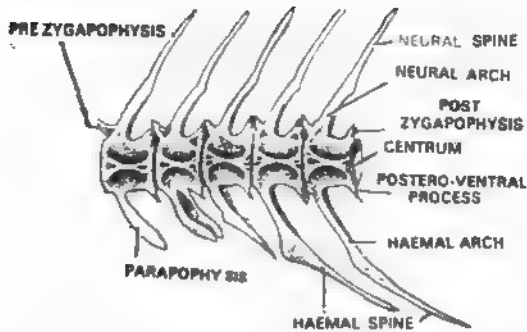


Fig. 4.7. Lateral view of the last precaudal and first four caudal vertebrae of *Labee*.

the fins. The dorsal fin has fifteen to sixteen lepidotrichia articulating with fourteen radials. Each radial consists of three pieces, a large dagger-shaped proximal segment (sometimes called inter-spinous bone of axonost), a short obliquely placed, mesial piece; and a smaller distal piece (Fig. 4.8A). The actinotrichia are slender, unjointed structures of horny consistency enclosed between the proximal ends of the lepidotrichia. The anal fin has eight fin-rays supported on seven radials.

The caudal fin is a large vertically expanded structure supported by a number of bony rods lying on either side of the urostyle. On the dorsal side of the urostyle lie three bony rods, two *epurals* (neural spines fused with radials) and one free radial. On the

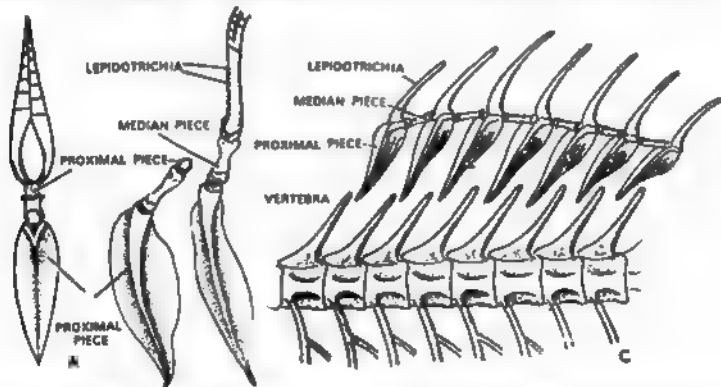


Fig. 4.8. A, radial and dermal fin-ray from front; B, two radials from the dorsal fin. C, side view of the dorsal fin with trunk vertebrae.

ventral side of the urostyle lie 9 *hypurals* (haemal spines fused with radials). The tail fin is represented by *hypochochordal lobe*, the *epichordal lobe* is small as the urostyle is turned upwards. It is divided into a dorsal and ventral portion. The dorsal lobe is supported by ten jointed finrays supported by the urostyle and four hypurals; and the ventral lobe is supported by five hypurals bearing nine fin-rays.

The *ribs* are a series of paired segmentally arranged bony rods, attached to the distal ends of the parapophyses of the trunk vertebrae. There are seventeen pairs of these and are sometimes called the *pleural ribs*.

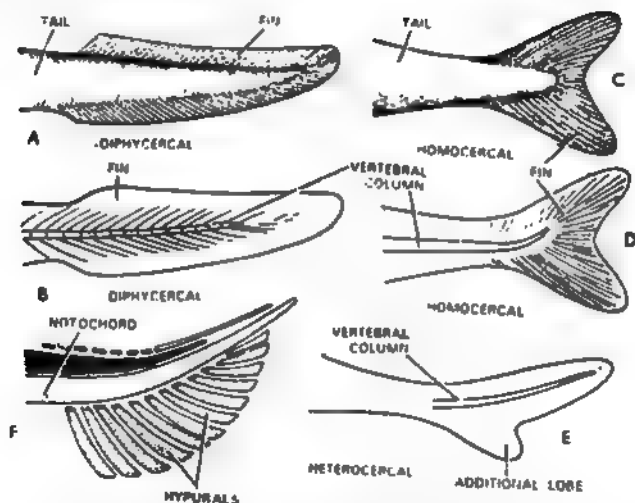


Fig. 4.9. A, B, Diphycercal caudal fin of fishes; C, external form of homocercal fin; D, internal structure of the same; E, external form of heterocercal fin; F, internal structure of the same.

Skull. The skull of the *rohu* is divisible into: (1) a posterior **occipital region**; (2) the **otic region** comprising the bones of the auditory capsules; (3) the **orbitotemporal region**; and (4) the **anterior nasal or ethmoidal region**.

The occipital region is formed by a **supraoccipital**, a **basioccipital** and a pair of **exoccipital** bones enclosing the **foramen magnum**. The supraoccipital forms the roof of the posterior part of the cranial cavity. It is divisible into a dorsal and postero-inferior portion. The dorsal portion is overlapped by the **parietals** in front and carries a vertical crest, the **occipital spine**, on its dorsal surface. It does not form the dorsal boundary of the foramen magnum. The exoccipitals are large bones each consisting of a **basal plate**, a large lateral **paroccipital process**, and a small dorsal process enclosing the foramen magnum. The basioccipital is a large drain pipe-shaped bone thickest in the middle. The posterior part of the groove of this bone is open and the anterior is covered by the **occipital condyle**.

The **otic region** consists of five bones, the **prootic**, **epiotic**, **sphenotic**, **pteric** and **opisthotic** in the adult teleosts. In *Labeo rohita* the opisthotic is absent in the adult probably fusing with the exoccipitals to form **par-occipital process**. The remaining four otic bones form a compact structure having the appearance of an inverted cup, one on each side of the hinder part of the cranial cavity. The **orbito-temporal region** includes: (a) **temporal or sphenoidal region**, and (b) the **orbits**. The sphenoidal region consists of the **parietal region** and the **frontal region**. The **parietal region** consists of a pair of dermal bones, the **parietals** forming the roof of the region. The sides of this region are formed by a pair of irregular bones, the **alisphenoids**, each consisting of a horizontal basal piece and a vertical process arising from the dorsal surface of the basal piece. Between the two basal pieces a V-shaped notch is left, both anteriorly and posteriorly, where it forms a part of the **pituitary fossa**. The floor is formed by the posterior part of the **parasphenoid**, the **basi-sphenoid** of other teleosts being absent in *Labeo* as a separate bone. The **frontal region** comprises the **frontals** forming the roof and occupying about one-half of the dorsal surface of the skull; the **orbitosphenoids** forming the floor as well as the middle portion of the inner wall of the orbit, and a long cross-shaped **parasphenoid** forming the floor of the cranium. In front the frontals articulate with the **mesethmoid** mesially and **nasals** and **ectethmoids** laterally. Along

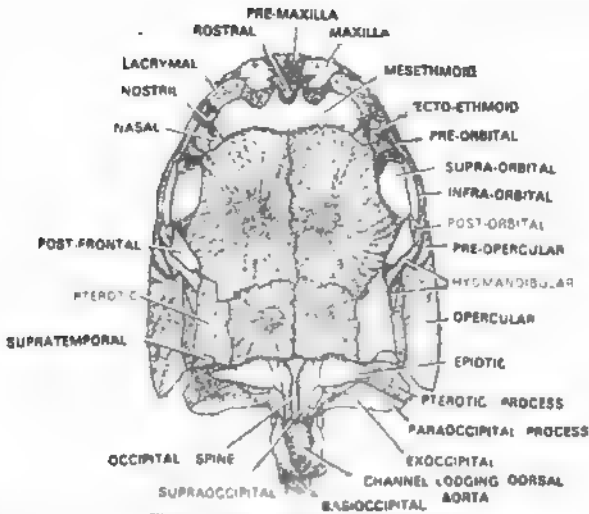


Fig. 4.10. Dorsal view of the skull of *Labeo*.

the antero-lateral edge it articulates with the supra-orbital, and the postero-lateral edge articulates with the post-frontal. Of these the **alt-** and **orbito-sphenoids** are replacing bones, the rest are all investing bones.

The orbits are two lying anteriorly in the ventro-lateral aspects of the skull. Each is

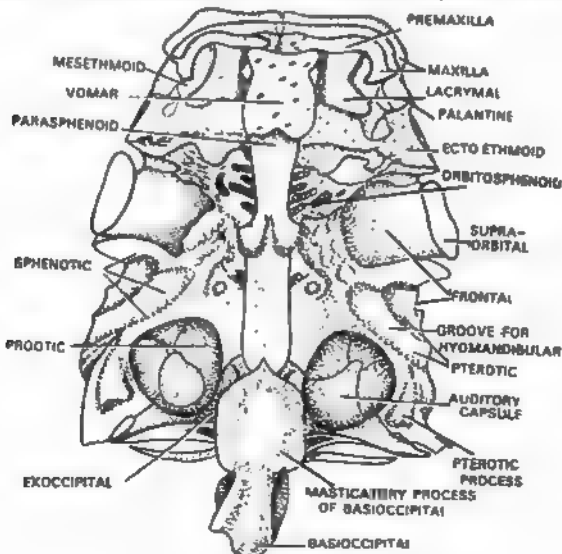


Fig. 4.11. Ventral view of the skull of *Labeo*.

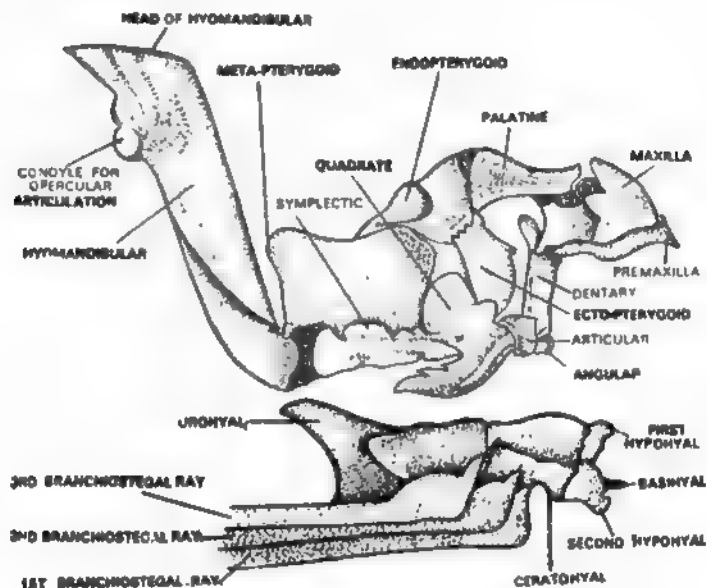


Fig. 4.12. Outer view of the right jaw and hyoid arch.

bounded by frontal dorsally, the ali- and orbito-sphenoids ventrally and mesially; the ectethmoid anteriorly and the sphenotic posteriorly. Besides these there is a definite orbital ring formed by five small orbital bones. The supra-orbital and post-frontal form the dorsal part of the ring, the pre-orbital forms the anterior boundary, the infra-orbital is antero-ventral and the post-orbital is posterior.

The nasal or ethmoid region comprises the paired nasals, the ectethmoids, lacrymals, and a median mesethmoid, a vomer and a rostral. The mesethmoid is a transversely elongated median bone lying in front of the frontal bones. It consists of a central piece drawn out into two lateral flat wing-like processes with rounded margins. The rostral is another median bone that fits into a concave notch on the anterior face of the mesethmoid. The vomer is a thin quadrangular bone lying on the ventral surface of the skull immediately in front of the parasphenoid and beneath the mesethmoid. The nasals are smaller reniform bones articulating with the postero-lateral margins of the mesethmoid and lying above the olfactory capsules, on either sides. The ectethmoid are paired bones forming the olfactory capsules on each side. Each ectethmoid possesses a deep nasal pit lodging the nasal sac and opening by double nasal opening. The lacrymals are situated along the antero-lateral borders of the mesethmoid, each being a small elliptical bone right in front of the nasal opening.

Foramina for Cranial Nerves. The Olfactory foramen for the exit olfactory nerve, is a large rounded aperture at the bottom of each olfactory capsule. For the exit of optic nerve there is a very large oval aperture the optic foramen, bounded dorsally by the alisphenoids, anteriorly by the orbitosphenoids and ventrally by parasphenoid. The oculomotor nerve passes out through a small elongated slit-like aperture the oculomotor foramen about a quarter of an inch behind the optic foramen. The pathetic foramen is a narrow elongated aperture toward the lower end of the alisphenoids, above the optic foramen and beneath the foramen for the ophthalmic division of the trigeminal nerve. The foramen for the ophthalmic division of the trigeminal is a fairly

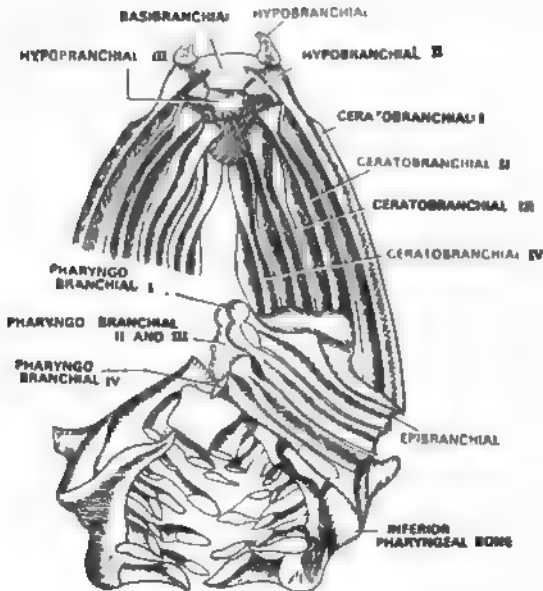


Fig. 4.13. Dorsal view of branchial arches.

large, more or less, triangular foramen lying at the posterior angle of the orbit above the foramen of the pathetic nerve. Below and a little behind the foramen for the ophthalmic division of the seventh nerve the large foramen for the main body of the fifth nerve perforates the prootic and lies immediately behind the large optic foramen. The abducens foramen is a small aperture between the oculomotor foramen and the foramen for the main body of the fifth nerve. The foramen for the ophthalmic division of the facial is a small rounded aperture on the inner wall of the orbit, above that of the ophthalmic division of the trigeminal. The facial foramen for the main division of the facial pierces the prootic just behind and below the foramen for the maxillary and mandibular divisions of the trigeminal. The glossopharyngeal and vagus emerge out through a large elliptical opening on the ventral surface of the posterior region of the skull, perforating the exoccipital just behind the prootic.

Visceral Skeleton. The visceral skeleton consists of seven visceral arches formed by the union of seven pairs of bony half-loops in the mid-ventral line. Of these arches the first is the mandibular arch, the second is the hyoid arch and the remaining five are the branchial arches. Four branchial arches support the gills, while the fifth forms the inferior pharyngeal bones. The mandibular arch (Fig. 4.13) comprises the primary palato-pterygo-quadrates closely related to the cranium forming (a) the primary upper jaw, and (b) lower jaw (Meckel's cartilage). The upper jaw in the adult consists of several bones formed by the ossification of the palato-pterygo-quadrates. The three bones that replace it include the palatine behind the maxilla, the metapterygoid a large quadrangular bone, and the quadrate, a more or less triangular bone which carries a ventral condylar process of the articulation of the lower jaw. Two dermal bones the ectopterygoid (pterygoid) and endopterygoid (meso-pterygoid) cover the primary jaw. The ectopterygoid is a triangular bone immediately behind the palatine and the endopterygoid is a thin rhomboidal bone lying behind the palatine and dorsal to the ecto- and meta-pterygoids. Two large investing bones, the maxillae, support the

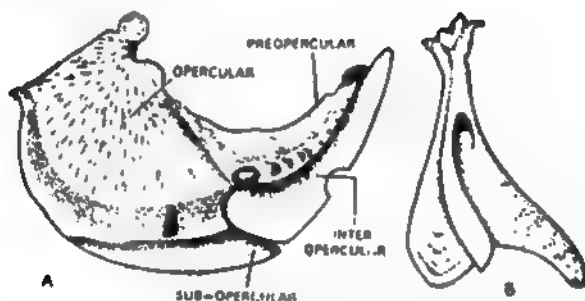


Fig. 4.14. A, external view of the operculum, B, side view of urohyal or basi-branchiostegal bone

anterior margin of the mouth on each side and form the secondary upper jaw. The **premaxilla** is a freely movable thick curved bone which meets its fellow in the middle line and forms the anteriormost bone of the skull. The **maxilla** is a thick curved bone of irregular shape lying parallel to the premaxilla partly overlapping it. They do not bear teeth. The lower jaw is formed by the ossification of Meckel's cartilage which forms **articular** and two other dermal bones, viz. the **dentary** and **angular**. The **articular** is a small vertically placed bone articulating with the quadrate. The **dentary** is a large hammer-shaped bone meeting its fellow from the opposite side in the median line. The **angular** is a small thick irregular bone that lies at the angle of the jaw and ventrally cover the lower end of the dentary with which it is mutually connected. None of these bones bear teeth.

The **hyoid arch** basically consists of two half loops, the **hyomandibular** and the **hyoid cornu** on each side. The first of these ossifies forming a **hyomandibular** bone above, articulating with the auditory capsule and simplectic bone below connected with the **quadrate**. These two bones form the **suspensorium**. The **hyoid cornu** ossifies forming three bones: the **epihyal**, the **ceratohyal** and a double **hypohyal**. The ventral median copula forms the **basihyal** connecting the hypohyal of the two sides. A small separate segment the **stylohyal** or **interhyal** lies between the simplectic of the dorsal hyomandibular cartilage and the epihyal of the ventral hyoid cornu. The ventral elements of the hyoid arch form the so-called **hyobranchial skeleton**.

Connected with the hyoid arch there are a number of investing bones supporting the operculum. These bones include a large **opercular**, a large **preopercular** partly overlapping the opercular, an elongated sabre-shaped **sub-opercular** lying below and internal to the opercular and a long stout **inter-opercular** lying all along the ventral border of the pre-opercular bone. Three sabre-shaped **branchiostegal rays** (branchiosts) are attached along the ventral border of the epi- and ceratohyals, while an unpaired bone, the **basibranchiostegal** or **urohyal** lies posteriorly to the basi-hyal.

The **branchial arches** are the remaining five pairs. Each branchial arch is ossified forming four replacing bones: a dorsal **pharyngobranchial**, a lateral **epibranchial**, a large ventral **ceratobranchial** and a small **hypobranchial**. In the third arch the hypobranchial forms an unpaired median piece. In the fourth arch the pharyngobranchial is unossified and hypo-branchial is absent. The fifth arch is reduced to a single bone, the **inferior pharyngeal bone**, on each side. This bone represents the enlarged **cerato-branchial**. Each is more or less triangular and lies in an oblique horizontal position behind the fourth arch. Its inner surface bears large and strong teeth arranged in three rows. These are the only bone bearing teeth in the **rohu**.

The **appendicular skeleton** consists of the **pectoral** and **pelvic girdles** along with the skeleton of their fins. The **pectoral girdle** consists of two distinct lateral halves which do not meet in the middle line. Each half (Fig. 4.15) is ossified into three replacing bones. The **scapula** is a ring-shaped bone lying laterally on the inner surface of the cleithrum (see the next page). The central foramen is the **scapular foramen** through

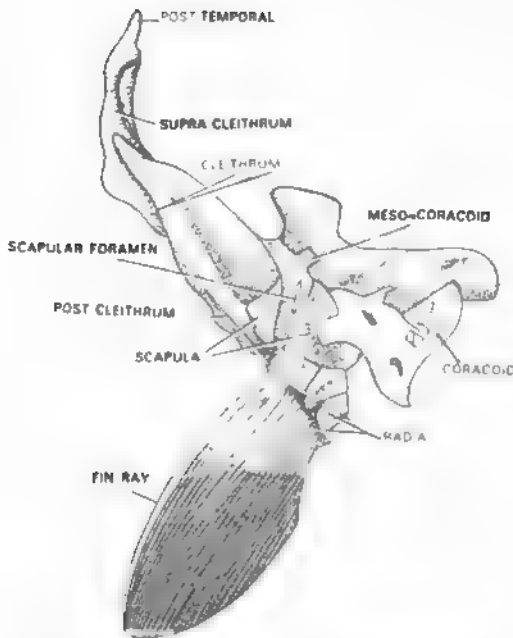


Fig. 4.15. Inner view of the left half of the pectoral girdle and fin.

which pass the branchial artery and nerve. The large irregularly triangular fenestrated **coracoid** bone lies in an obliquely ventral position internal to the scapula and ventral to the **mesocoracoid**, which is an inverted Y-shaped bone lying closely attached to the inner surface of the cleithrum. The scapula and the coracoid both share in the formation of the glenoid fossa. Many dermal bones invest the girdle and form the so-called secondary girdle. These include (a) the **cleithrum**, (b) the **supracleithrum**, (c) the **post-temporal**, and (d) the **post-cleithrum**. The cleithrum or **clavicle** is the largest and most prominent crescentic bone completely covering the primary girdle on the outside. The **supracleithrum** is a dagger-shaped bone articulating with the outer surface of the dorsal end of the cleithrum. The **post-temporal** is a small conical bone articulating with the **supracleithrum** at its dorsal end. The **post-temporal** fits into a groove on the dorsal surface of the pterotic and articulates anteriorly with the **supratemporal**. A small bone, the **supratemporal**, partly overlaps the **post-temporal**.

The skeleton of the **pectoral fin** consists of four **radials** supporting nineteen **dermal fin-rays** or **lepidotrichia**. The radials articulate with the girdle at the **glenoid fossa**. The first three radials carry four rays each, while fourth carries seven rays. The fin-rays decrease in size from preaxial to the post-axial margin.

Each half of the **pelvic girdle** consists of a **pelvic bone** lying in the ventral body wall. A small piece at the hind end of the original cartilage remains unossified. Each pelvic bone is forked anteriorly and continues posteriorly into an elongate piece of cartilage. The pelvic fin consists of three small radials supporting nine fin-rays which are long slender jointed bony rods. The first radial is a double triangular piece carrying two rays. The second radial is also a double piece, slightly larger than the first, carrying two fin-rays. The third radial is the largest and carries five fin-rays.

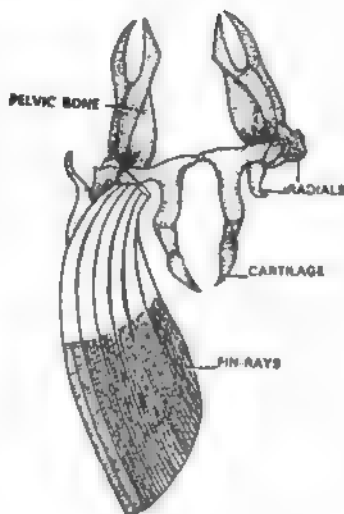


Fig. 4.16. Ventral view of the pelvic girdle and the right pelvic fin.

DIGESTIVE SYSTEM

The digestive system (Fig. 4.17) comprises the organs concerned with the capture, digestion and absorption of food. The alimentary canal and its associated glands such as the liver and pancreas constitute the system. The alimentary canal is an extremely long tube beginning at the mouth and terminating at the anus. In fact the intestine is usually very long in herbivorous fishes and short in carnivorous ones. It is differentiated into many parts: the mouth, buccal cavity, pharynx, oesophagus, stomach, intestine and rectum.

The mouth is bounded by soft lips being just vertical folds. The free margins of the lips are broader and densely covered with four or five rows of darkly pigmented conical papillae. The inner fold of each lip is narrow, muscular and without papillae. The buccal cavity is a dorso-ventrally depressed cavity with a slightly arched roof and a more or less flat floor. The thick mucous membrane lining the cavity is covered with minute papilla-like outgrowth. The mucous membrane of the floor is lined by thick muscles, but a distinct tongue is absent. The pharynx (Fig. 4.18) is also dorsoventrally flattened cavity bounded by gill-arches on the side and extending a little beyond the pharyngeal teeth. The whole structure is divided into two parts, an anterior and a posterior pharynx. The anterior pharynx is narrow in front but wide behind. It is perforated on the sides by gill-slits, through which it communicates with branchial chamber. The mucous membrane is thick bearing papillae. The branchial arches are supported by minute gill-rakers meant to filter the water. The posterior pharynx follows the anterior pharynx, the latero-ventral wall of which are beset with pharyngeal teeth, while the median region of the floor is lined with transversely folded mucous membrane.

The pharyngeal teeth are strong crushing closely-set teeth arranged in three rows, the teeth of one row alternating with those of the other. Their grinding surface are truncate and pressed against each other forming a common semicircular chewing area on either side. The teeth are homodont (all alike). Each tooth consists of a basal root

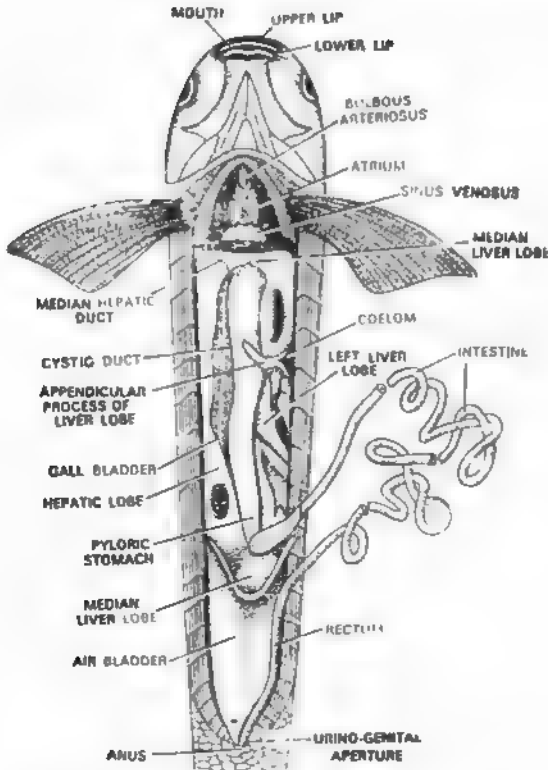


Fig. 4.17. Visceral organs of *Labeo rohiti* (after Sarabhai).

(Fig. 4.19) buried in the mucous membrane and fused with the bone below, and a crown projecting in the pharyngeal cavity. The root is narrow, cylindrical, above and broader at the base. It is hollow and contains a large pulp cavity (Fig. 4.19 D). The crown is laterally compressed. In addition to the functional teeth various stages of developing teeth also occur imbedded in the mucous membrane, behind and between the functional teeth. The new teeth have enamel covering the dentine of the crown but in the older ones the enamel gets worn off and dentine becomes visible at the cutting surface. In *Labeo* the pharyngeal teeth are also employed to crush the hard and solid food masses.

The oesophagus (Fig. 4.18) is a narrow, thick, and short tube about an inch long and quarter of an inch in diameter. The inner lining of oesophagus is raised into seven prominent longitudinal folds and several smaller folds. From the dorsal side of the oesophagus arises the pneumatic duct leading into the air bladder. The opening of the oesophagus in the stomach is guarded by a valve like structure formed by an overgrowth of the folds of mucous membrane of the oesophagus. The stomach (Fig. 4.18) is the next part of the alimentary canal. It lies dorsal to the coils of intestine proper and ventral to the airbladder. The large liver lies on its either side. It is more or less thick straight tube with a slight curvature about the middle of its length. The

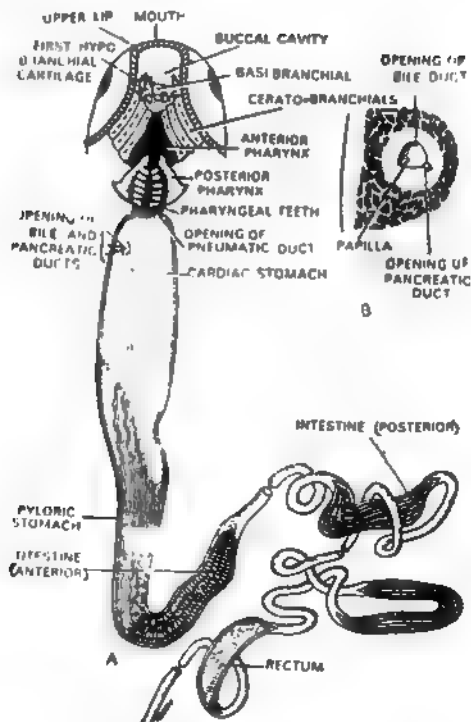


Fig. 4.18. Digestive organs of *Labeo*. A, alimentary canal; B, papilla magnified to show the opening of bile and pancreatic ducts.

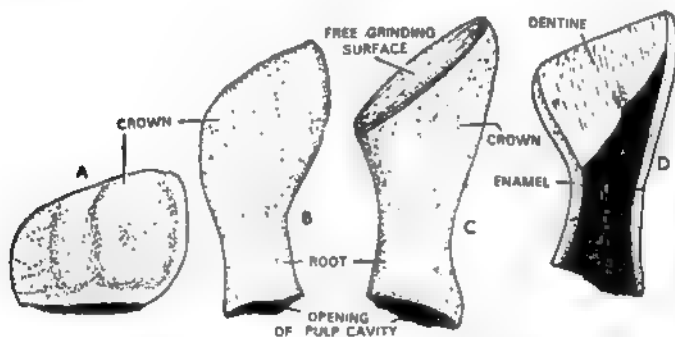


Fig. 4.19. Pharyngeal teeth of *Labeo*. A, growing tooth; B, fully formed tooth; C, side view of B; D, sagittal section of the same (after Sarbahi).

stomach is divisible into two regions, the **anterior cardiac region** and the **posterior pyloric region**. The mucous lining of the cardiac region presents a honeycomb appearance, while that of the pyloric region is raised into a number of thick longitudinal folds. Posteriorly the stomach curves to the left and passes into the intestine. The pyloric caeca, so characteristic of the teleostean fishes, are altogether absent in *Labeo rohita*. The **intestine** (Fig. 4.18) is a thin-walled tube of more or less uniform diameter disposed into a large number of coils, and fills up the entire ventral portion of the abdominal cavity. The mucous lining of the anterior region of the intestine is folded forming low obliquely transverse ridges and those of the posterior region are distinctly longitudinal. The intestine attains a length of over twenty-eight feet. The **rectum** is a thin-walled sac, wider than the intestine, and opening to the outside at the anus, situated in front of the urinogenital opening. The mucous membrane presents inconspicuous oblique transverse folds, hardly visible to the naked eye.

Glands of Digestion. The liver (Fig. 4.20) is a solid elongated gland of dark brown colour consisting of two lobes, the right and left. The right lobe is narrow and elongated and the left lobe is broader. The two lobes are connected to each other at three places by transverse connections: (a) an anterior **median lobe** connects the two in the cardiac region of the stomach and lies ventrally, (b) the **middle connecting lobe** lies on the dorsal side of the stomach just where the cardiac and pyloric regions pass into each other, (c) the posterior **median mass** is a more or less crescentic lobe at the posterior ends of the liver lobes.

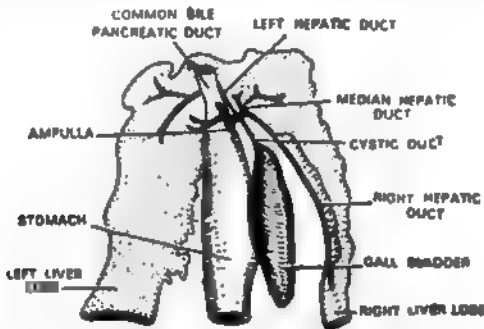


Fig. 4.20. Liver and gall-bladder of *Labeo* (after Sarbajit).

The **gall-bladder** (Fig. 4.20) is a thin-walled elongated sac wedged in between the right lobe of the liver and the cardiac portion of the stomach. It is about three inches long and about an inch in diameter. From the antero-ventral end of the gall-bladder arises a broad thin-walled **cystic duct**, that receives three ducts from various parts of the lobes of the liver and finally opens into the stomach. After receiving the three ducts the cystic duct is known as the **bile duct**. The short bile duct runs side by side with the pancreatic duct, in fact the two ducts are enclosed in a common sheath.

The **pancreas** is apparently absent in the *rohu*, but is really present as diffuse mass scattered, more or less, all over the visceral cavity and also imbedded within the substance of the liver. It is also found as a **perivascular tissue** surrounding the finer branches of the blood vessels ramifying in the adipose tissue. It is also imbedded in the substance of the spleen. It cannot be recognized in dissections but only in microscopic preparations. The **pancreatic duct** formed by the union of small ductules arising from pancreatic tissues, emerges from the anterior part of the left hepatic lobe, runs along with the bile duct, and opens in the anterior part of the cardiac stomach (Fig. 4.17).

Ductless Glands. The spleen consists of a large number of distinct dark red lobes of

various shapes and sizes scattered in the adipose tissue surrounding the gut. Most of the lobes are aggregated together in a shallow depression on the ventral surface of the left hepatic lobe in close proximity to the stomach. The **thyroid** is a diffuse mass of glandular tissue lying associated with connective and lymphoid tissues surrounding the ventral aorta in the region of the first afferent branchial arteries. It can only be seen on a careful microscopic examination. The **thymus** is an elongated strip of connective tissue lying obliquely on either side in the region of the first and second vertebrae on the postero-dorsal surface of the inferior pharyngeal bone in the fifth arch. Its posterior end lies just in front of the large mass of the head-kidney, while its anterior end, which is uppermost, almost reaches the postero-ventral edge of the ex-occipital bone.

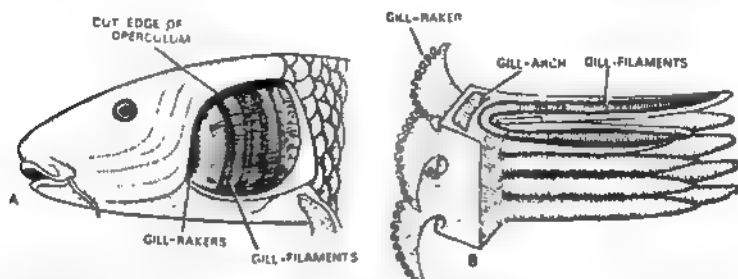


Fig. 4.21. A, operculum removed to show gills in the branchial chamber; B, diagrammatic sketch of the gill-filaments.

AIR-BLADDER

A thin-walled sac, filled with gases, called air or **swim-bladder** lies in the body cavity, dorsal to the alimentary canal and ventral to the vertebral column. The air-bladder (Fig. 4.16) is a large air-filled sac made up of two chambers, an anterior and a posterior. Externally a deep constriction separates the two. The anterior chamber is connected to the alimentary canal, just at the beginning of the oesophagus, by a slender **pneumatic duct**. The air-bladder acts as a hydrostatic organ to adjust the specific gravity of the fish to that of water at different depths.

RESPIRATORY SYSTEM

The **gills** (Fig. 4.21A) are contained in a common chamber one on each side of the pharynx. They are united proximally but their distal ends are free and the inter-branchial septa are practically obsolete. Each gill bears a double row of **branchiae** or **gill-filaments** each of which bears many minute transverse plates covered with thin epithelium containing capillary network existing between the afferent and efferent branchial arteries. Each gill is supported by a cartilaginous **gill-arch**, the inner border of which expands to form flap-like **gill-rakers**, that protect the gills from hard particles and do not allow food from passing out through the gills. The vestigial gill of the hyoid arch (**pseudobranchia**) consists of a small comb-like body, formed of a single row of gill-filaments situated on the inner surface of the operculum.

CIRCULATORY SYSTEM

The **pericardial cavity** is a more or less triangular anterior portion of the coelom enclosing the heart. The heart is like that of the dogfish in essential details comprising a **sinus venosus** emptying into a thin-walled **auricle** or **atrium**. The **ventricle** is muscular and into it opens the atrium. The heart is without **conus arteriosus**, but the base of the

ventral aorta becomes dilated forming a **bulbus arteriosus**. All the parts, as usual, are separated by valves to prevent backflow of blood.

Afferent Branchial Arteries. The anterior continuation of the bulbus arteriosus or the **ventral aorta** (Fig. 4.22) runs forward, along the ventral surface of the pharynx, right up to posterior end of the hyoid, where it bifurcates into two **afferent branchial arteries**, one going to the right and other to the left. The first afferent branchial (Fig. 4.22) arises by the bifurcation of the ventral aorta itself and runs along the first gill distributing to the capillaries in the gill-filaments. A little distance behind the first arises the **second afferent branchial** (Fig. 4.22) from the ventral aorta and loops back to enter the second gill. The **third afferent branchial** (Fig. 4.22) arises from the aorta behind the second, the distance between the second and third being more than that between the first and second. The **fourth afferent branchial** (Fig. 4.23) arises behind the third, the third and fourth being almost as much apart as the first and the third. The distance between the fourth branchial and the conus is as much as that between the fourth and the first branchial. It supplies the fourth gill.

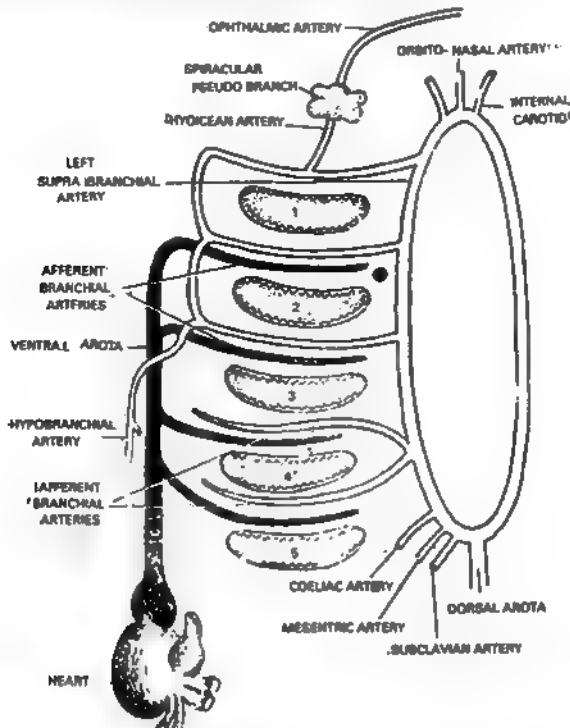


Fig. 4.22. Afferent and efferent arteries of a teleostean fish.

Efferent Branchial Vessels. In the teleostean fishes each gill-arch has a single afferent and single efferent branchial artery quite unlike the dogfish in which each gill-arch has two efferent branchial vessels. The dorsal aorta (Fig. 4.24) is formed by the union of two lateral aortae (radices aortae) that retain their separate identity up to the level of the second gill-arch. From the point of union of the two aortae the dorsal aorta proceeds behind and runs along the entire length of the body giving rise to

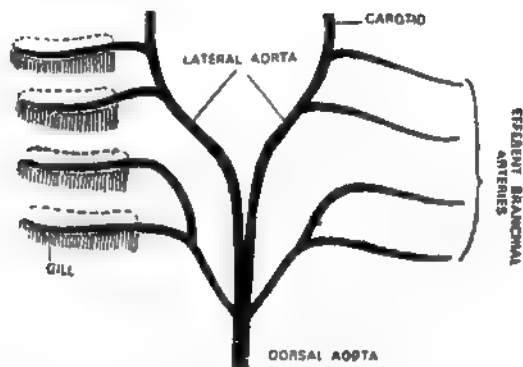


Fig. 4.23. Efferent arteries in *Labeo* forming the dorsal aorta.

several arteries to various organs of the body. The first efferent branchial (Fig. 4.24) artery meet, the lateral aorta in the region of the first gill from which it emerges. The lateral aorta proceeds anterior to the junction of the first efferent branchial as the carotid trunk and enters the cranium. The second efferent branchial comes from the second gill and meets the lateral aorta a little behind the first. The third and fourth branchial arteries returning blood from the third and fourth gills respectively unite and open into the dorsal aorta by a common stem. From the dorsal aorta arise several blood vessels prominent among which are the subelavian, coeliaco-mesenteric, posterior mesenteric, parietal, renal and iliac arteries.

The principal veins include the paired anterior cardinals and posterior cardinals and unpaired hepatic portal leading through the liver. The renal portal system is well developed and collects blood from the tail region. There are some segmental veins collecting blood from the trunk segments and pouring it into posterior cardinals which are connected, in some cases, by transverse anastomosis in the region of the kidney. The subelavian collects blood from the region of the pectoral fin. In these animals the ventral abdominals of the elasmobranch fishes are lacking. All the main veins are large in diameter but not so big as in the elasmobranchs. As mentioned above there is no muscular conus arteriosus, but only a thin bulbus arteriosus at the base of the ventral aorta. The walls of the bulbus are elastic but not muscular. It dilates with each beat of the ventricles and is able to maintain the pressure of the capillaries only. It is not understood how the circulation is maintained. Probably the circulatory system "works at the disadvantage of a low venous return pressure, but it is not understood how this has been overcome" (Young). The blood of fishes is pale as compared to that of the terrestrial animals. It is lesser in quantity also. The fluid plasma contains nucleated oval red cells or erythrocytes and various types of white cells or leucocytes.

NERVOUS SYSTEM

Brain. The brain of the *rohu* is different from that of the dogfish being more specialised. The prosencephalon is small and undivided (seen dorsally), hence separate cerebral hemispheres are not formed. The pallium or the roof of the prosencephalon is non-nervous and the floor is raised to form a prominent thickening, the corpora striata. Anteriorly it is continued into the olfactory bulbs. The diencephalon is much reduced, indicated only by the origin of the stalked pineal body dorsally which is not eye-like. The optic lobes are large and appear most prominent in the whole brain. On the ventral surface of the optic lobes are large bean-shaped lobes the lobi inferiores. The cerebellum is very large and bent on itself. The anterior part of the cerebellum is

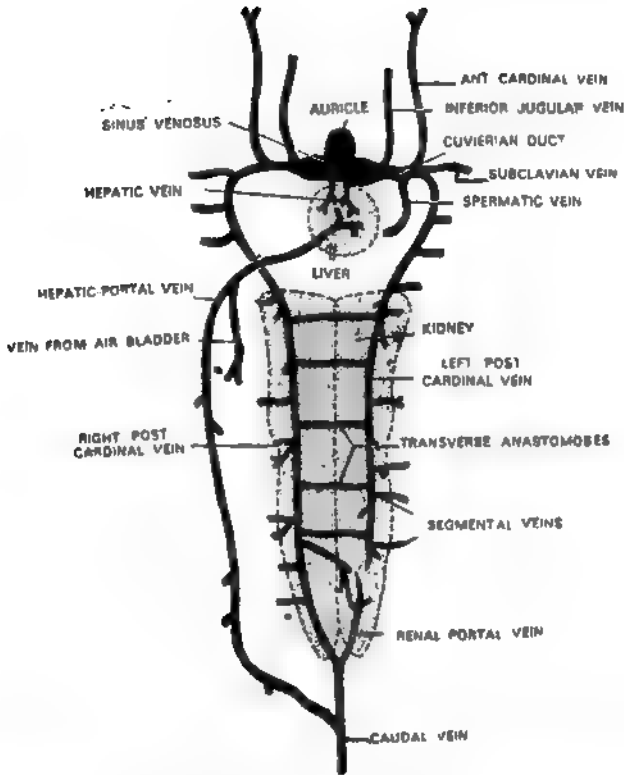
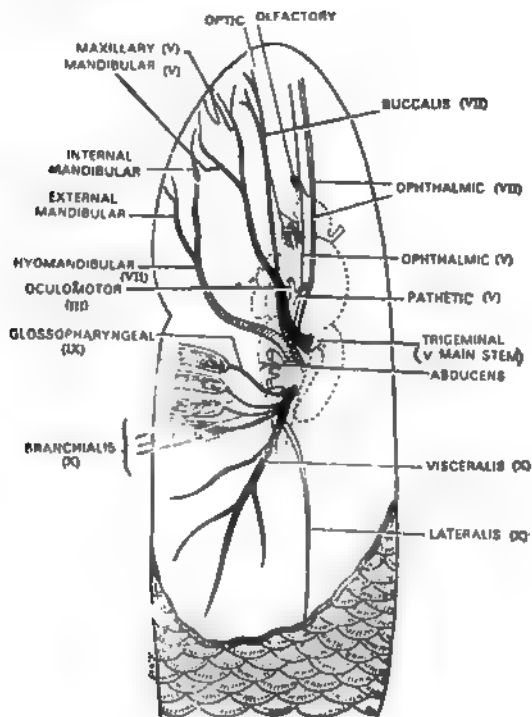


Fig. 4.24. Venous system of a typical teleost.

pushed forwards under the roof of the mesencephalon to form the *valvula cerebelli*, a teleostean characteristic. The optic nerves do not form a chiasma, but simply cross one another, one going to right and the other to the left. The *pituitary body* is a rounded structure lying just behind the crossing of the optic nerves. Behind the pituitary body lies a small body the *sacculus vasculosus*. Three transverse bands of fibres connect the right and left halves of the fore-brain, (a) The *anterior commissure* joining the corpora striata; (b) the *posterior commissure* located just behind the pineal body; (c) the *inferior commissure* situated in front of the infundibulum.

Cranial Nerves. There are ten pairs of cranial nerves, as in the dogfish, that are similarly disposed. The *ophthalmic nerves* (Fig. 4.25) are the two nerves running across the dorsal margin of the orbit. In fishes in general the ophthalmic nerve is formed by the intimate association of the ophthalmic branch of the fifth or trigeminal nerve with the ophthalmic branch of the seventh or facial nerve. The ophthalmic here is represented by two separate branches: (a) *ophthalmicus superficialis* running dorsally, and (b) *ophthalmicus profundus* running below. The *trigeminal nerve* divides into three branches. (a) *ophthalmic* (described above), (b) *maxillary*, and (c) *mandibular*. The maxillary runs along the posterior margin of the orbit. After running a little from the place of its origin it bifurcates into two: the *maxillary proper* that turns

Fig. 425. Cranial nerves of *Labeo rohita*.

towards the anterior end of the upper jaw innervating the skin and muscles of that region, and the **mandibular** that crosses the angle of the jaws to innervate the masticatory muscles, gum and teeth of the lower jaw, and integument of the region. The **facial** or seventh nerve arises just behind the fifth and soon divides into three main branches: (a) the **ophthalmicus superficialis** (described above), (b) the **buccalis**, and (c) **hyomandibular**. The **buccalis** runs obliquely downwards and forwards across the orbit from the place of its origin, as in the dogfish, and innervates the associated regions. The **hyomandibular** branch runs backwards and outwards and divides in a **mandibularis externus**, a **mandibularis internus** and a **hyoideum**. The **palatine** is another branch of the seventh that runs across the floor of the orbit to the palate. The **glossopharyngeal** or ninth arises from the ventrolateral surface of the medulla, runs obliquely backwards and on reaching the first gill, which it innervates, it divides into two branches: a **pretrematic** running along the anterior border of the gill, and a **post-trematic** running along the anterior border of the gill. The **tenth** or **vagus** divides, immediately on emerging, into three branches: (a) the **branchialis** which gives off branches innervating the remaining gills; (b) the **visceralis** the main branch that enters the body cavity and supplies the various organs of the viscera; and (c) the **lateralis** that turns backwards and runs parallel to the lateral line, buried deep in the tissue. The **olfactory**, **optic**, **oculomotor**, **trochlear**, **abducens** and **auditory** have not been included in the description above. Their position and relationships are similar to those of the dogfish.

The structure of the spinal cord is typical. It is covered by neural arches and gives off spinal nerves, one to each body segment. Each spinal nerve arises by two roots, one dorsal and one ventral. The number of spinal nerves depends upon the number of body segments.

Sense organs. The sense of taste is highly developed and is centred in the numerous and well-developed **taste-buds**, which are distributed on the inside and outside of the lips, in the lining of the first three gill-slits, on the barbels, and in some teleosts in groups over the external surface of the body even on the tail (not checked in the *rohu*). The tactile receptors are distributed all over the epidermis, but they are particularly abundant on the lips and barbels. The dorsal **olfactory sacs** on the snout contain cells sensitive to substances dissolved in water. A well-developed pressure and water-vibration sense is located in the **lateral-line system**, which extends over the head and is innervated by the *lateralis* branch of the tenth cranial nerve. Slight changes in pressure or slow wave or current movements are detected by this system. This system, it is believed, survives in land vertebrates as the inner ear.

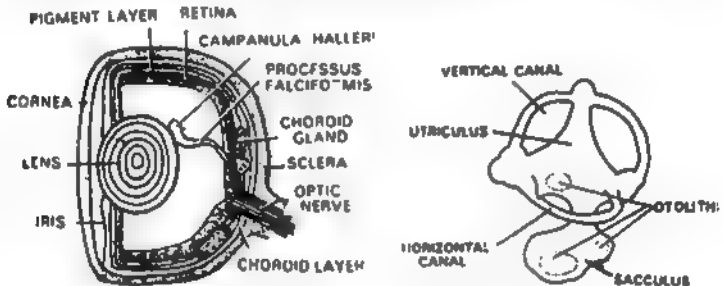


Fig. 4.26. A, structure of the eye of a teleost. B, The ear of teleost.

Eye. The eye presents typical vertebrate plan of structure except in a few characteristic points. The cornea is flat and is, more or less, in contact with the lens, which is globular, thus reducing the aqueous chamber. There is a silvery layer, the **argentea** between the cartilaginous **sclerotic** and the vascular **choroid**. It acts as a reflector. The silvery colour is due to the presence of minute crystals of that colour in the cells which constitute the **argentea**. The **choroid process** is lacking, but a **falciform process** is present. It is vascular fold of choroid that pierces the retina near the entrance of the optic nerve and continues up to the lens where it ends in a knob, the **campanula Halleri** (Fig. 4.26). In other details the eye presents typical vertebrate structure. The large eyes probably focus clearly on nearby objects, but also serve to detect moving objects above water, such as a person walking on the bank.

Ear. The ear presents the structures as found in the dogfish - the **utricle**, **sacculus**, **lagena** or **cochlea**, which is rudimentary, and the **semicircular canals**. The main difference is in the remarkably large size of the **otoliths** which are three in number: (i) the **sagitta** is the largest (being 6 mm. in *Salmo*) and fills the **sacculus** (Fig. 4.26 B); (ii) the **asteriscus** is a small granule situated in the **lagena** (Fig. 4.26 B); (iii) the **lapillus** is the third placed in the **utricle** close to the **ampullae** of the anterior and horizontal canals (Fig. 4.26 B).

It is extremely doubtful whether fishes can "hear". They, however, respond to certain types of jarring or vibration by means of their lateral-line organs. Any vibrations that are perceived by the internal ear must be transmitted through the head or body because the fishes do not have eardrums or middle ear.

Autonomic System. The autonomic nervous system is different from that of the **elasmobranch fishes** and also from that of the **terrestrial animals**. The chain of **sympathetic ganglia** extends from the level of the **trigeminal nerve** backwards, a **ganglion** is found in connection with each **cranial dorsal root**. In **elasmobranch** there is

no sympathetic system in the head. The sympathetic ganglia do not receive pre-ganglionic fibres from the segments in which they lie but by fibres which run out in the ventral root of the trunk region and thence forwards in the sympathetic chain. Each trunk sympathetic ganglion, besides receiving a white ramus communicans of pre-ganglionic fibres from its spinal nerve, also sends a grey ramus back to that nerve. This grey ramus carries post-ganglionic fibres to the skin. Some of these fibres have been shown to control the melanophores (colour cells), causing them to contract as a result of which the skin becomes paler. In fact the teleosts are the vertebrates that change their colour most quickly and completely. This colour change is brought about by the movement of pigment in the processes of the melanophores. These post-ganglionic sympathetic fibres thus bring about the colour change in fishes. Little is known about the parasympathetic system of the bony fishes.

Urinary Apparatus. The kidneys (Fig. 4.27) are large reddish brown structures extending along the whole length of the abdomen, dorsal to the air-bladder, and partly

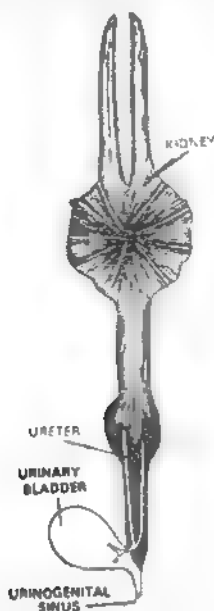


Fig. 4.27. Kidneys, ureters and urinary bladder of *Labo*.

fused together in the middle line. They are derived from the mesonephros of the embryo. The fluid nitrogenous wastes are removed from the blood and are carried by the ureters (mesonephric ducts) that emerge out of the posterior part of the kidney, one on each side, and both empty into a thin-walled urinary bladder. The urinary bladder is a thin-walled sac lying ventral to the cloaca and opening into the urinogenital sinus.

In the fresh water fishes there is a tendency to gain water and lose salt, because the concentration of salt in the blood is more than that in the surrounding. The glomeruli are numerous and have excellent filtration system. This eliminates all the excess water that enters the system. The skin is not highly vascularised and is an almost waterproof layer. The production of mucous aids waterproofing. Thus the water cannot enter through general waterproof surface nor can salt pass out. Whatever water gets in, is

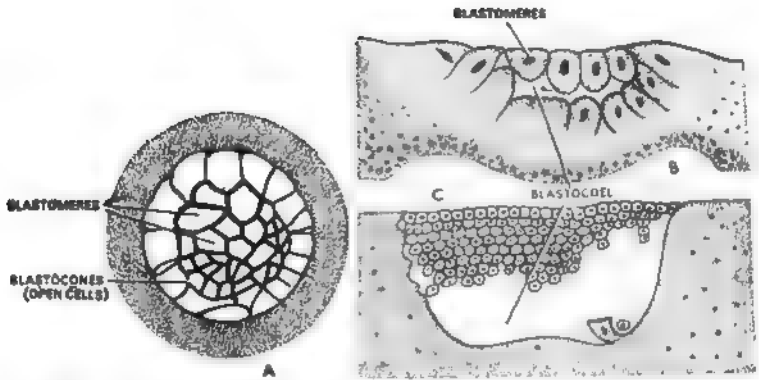


Fig. 4.28. Segmentation in a bony fish. A, blastoderm dividing, surface view; B, and C, sections of the embryos showing the blastocoel.

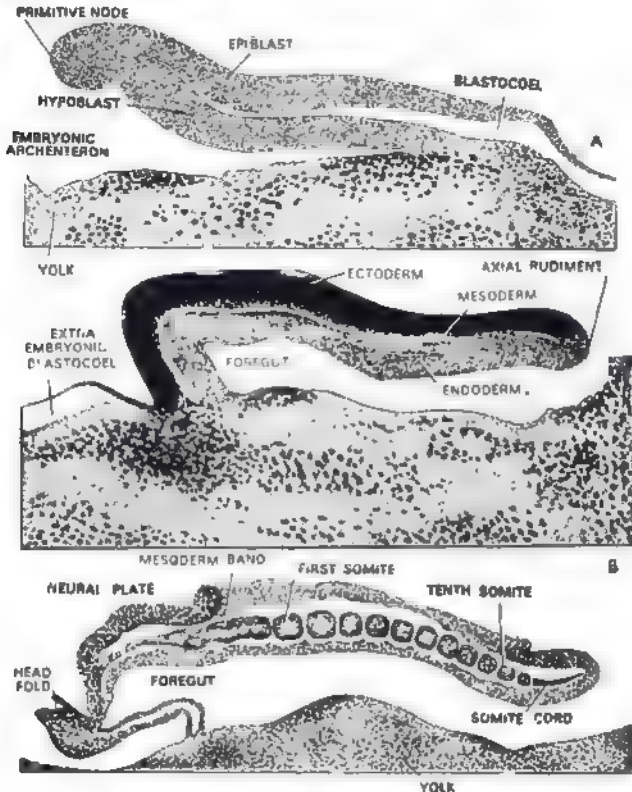


Fig. 4.29. Section of the embryo of a bony fish.

removed by the active glomerular filters. Then there are certain special tubules developed for reabsorption of salts. Thus the amount of salt that is passed out is reabsorbed and the balance is maintained. The kidney, therefore, is not only the organ of elimination of nitrogenous waste but an organ of regulation of the quantity of water (osmo-regulation) in the body and maintenance of salt proportion inside the body.

In the marine teleosts the problem is just the opposite. In the sea water the concentration of salt in the water outside is more than that in the blood. The balance is maintained by the reabsorption of urea and by taking in water and salts and then excreting the salts. For this purpose special chloride-secreting cells are present in the gills, they dispose of the excess salts.

Reproductive Organs. The gonads become quite large in sexually mature forms. In the male the testes, in the breeding season, are long smooth pinkish organs extending the whole length of the abdominal cavity. From the posterior edge of each testis arises the *vas deferens*, a duct that runs posteriorly finally opening into the *urinogenital sinus*. At mating the "milt" or spermatic fluid passes in the *vasa deferentia* finally emerging from the urino-genital aperture. In the female the ovary runs along the full length of the abdominal cavity and each is relatively larger than the testes. The ovaries are covered with peritoneum and ova are released in the body cavity. The oviducts are lacking. The anterior wall of the urino-genital sinus is pierced by a pair of *genital pores*, through which the ova emerge out. In some bony fishes the oviducts exist and it is through them that the eggs pass out.

In the majority of teleosts the eggs float near the surface of water (pelagic eggs) and in others (*rohu*) they sink to the bottom (demersal eggs). Such eggs are tiny translucent objects which are laid in enormous numbers. It has been estimated that an average female cod may contain at the breeding season about 6,500,000 eggs. Most of these are destroyed, only a few are able to develop. Eggs are usually small and the time required for development varies with the species and with the temperature of water.

The *rohu* breeds in rivers and in "bunth" type tanks during the time of monsoon (July to September). The eggs are small and laid in large numbers. As the eggs are laid, the milt is passed over the eggs rather simultaneously. The sperms of *rohu*, it is reported, cannot survive for a long time, therefore, fertilization takes place as soon as the eggs are laid. Nothing is known about the cleavage and the development of *Labeo*, but collected eggs present the different stages of development of the embryo and that suggest that the development should be like that of any other teleost. The description given below is the account of the development of *Salmon*.

The ovum is covered by a thick membrane, the *zona radiata*. A small aperture, the *micropyle*, perforates it. The sperm enters through the micropyle. The protoplasm accumulates at one pole forming an elevated *germinal disc*. The cleavage is meroblastic being confined to the germinal disc. Before cleavage begins the germinal disc usually shows amoeboid movement. As a result of cleavage a superficial sheet of cells, the *blastoderm* (Fig. 4 28), is formed. As the cleavage proceeds further a segmentation cavity is formed under the blastoderm (Fig. 4 28).

Now an infolding begins at the posterior edge of the thickened embryonic blastoderm which here becomes continuous with the cells of the lower layer. The cavity formed below this infolding (Fig. 4 29) is the rudiment of the *archenteron*, which is small at first but becomes larger later. The upper lining of this cavity forms a continuous layer the *endoderm* (Fig. 4 29) with further growth the endoderm grows and the original blastocoel becomes smaller and smaller finally disappearing. In between these appears the *mesoderm band* which breaks up into definite sinuses.

The embryo arises as an elevation growing forwards from the thickened edge of the blastoderm, and, as it increases in length, it appears as a clear colourless band winding round the yellow yolk. Open medullary groove is not formed. As in the lampreys the nervous system is formed from a fold of ectoderm, the walls of which are in apposition so as to form a keel-like ridge. The head and tail develop gradually and become free from the yolk (Fig. 4 31). When the embryo hatches it is transparent and the yolk-sac is suspended underneath its body (Fig. 4 30). The young are quite small upon hatching and gradually assume the adult form.

Time of hatching varies in different carps. In *Labeo rohita* the eggs hatch within a

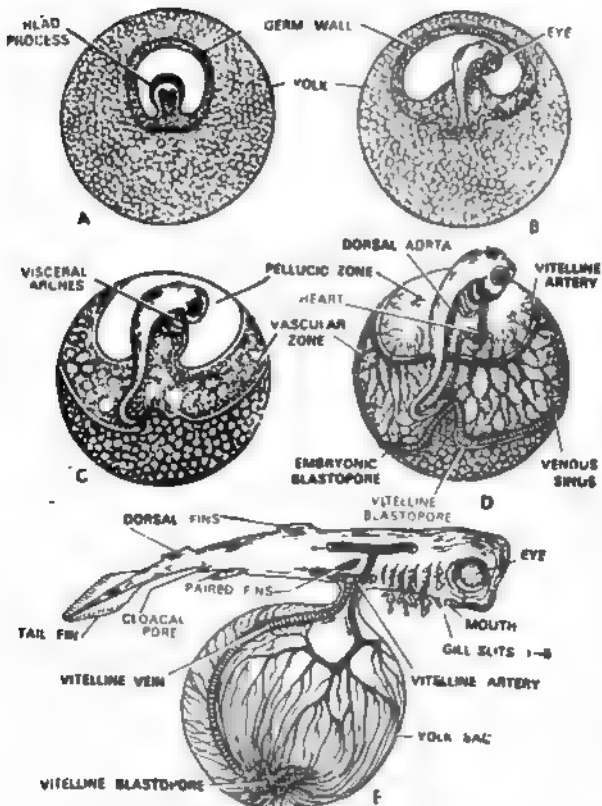


Fig. 4.30. Further stages in the development of a bony fish.

period of two to fifteen hours. The young ones that hatch out (hence called **hatchlings**) have conspicuous yolk-sac attached ventrally and are about 4 to 5.5 mm. long. The hatchlings subsist on the yolk in the yolk-sac for at least two days. Usually 5 days to a week is taken for the absorption of yolk. After this period they begin to feed on organism contained in the water. These young ones are often referred to as fry. The young carp fry are about $\frac{1}{4}$ to 1 inch long and are distinguished from other fry by their fringed lips, dorsal fin-rays and a conspicuous vertical blotch-like dark spot at the base of the tail which disappears with growth. When the fry attain a size of 2 inches they are called **fingerlings**. The fingerlings vary in size from two to six inches. *Labeo rohita* is quite a quick-growing carp although perhaps it grows, relatively a little slower than the other carp catla (*Catla catla*). Within a year, under normal circumstances, it attains a size of fourteen to sixteen inches. Sexual maturity is attained towards the end of the second year, it grows to over three feet in length in some cases.

Other Carps. Most of the cyprinoid fishes (belonging to the suborder Cyprinoidea) are known as carps. In India the carps are of great importance as they constitute a major percentage of human food. The best known carp is the catla (*Catla catla*), then comes the rohu (*Labeo rohita*). The genus *Labeo* has several Indian species. The rohu

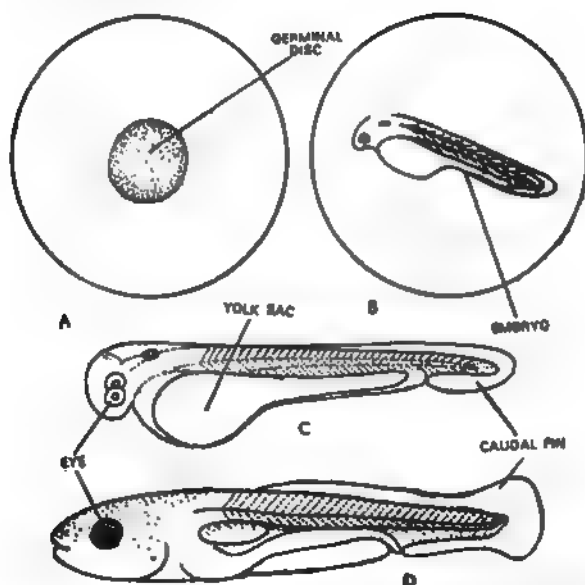


Fig. 4.31. Stages in the development of a carp. A, fertilized egg with fully swollen egg membranes; B, young embryo fairly well developed; C, young fish just hatched; D, young fish two days after hatching. Figures from different stages collected from rivers and ponds.

itself is considered to be a tastier fish than any other Indian carp. The *kalbasu* *Labeo calbasu* is another species of *Labeo* that is equally popular and easily available in Uttar Pradesh. *Labeo fimbritans*, *Labeo kontius*, *Labeo bata*, *Labeo gonius*, *Labeo nandina*, *Labeo dussumieri* are other species of this genus. Then there is the *mrigal* (*Cirrhina mrigala*), the white carp (*Cirrhina cirrhosa*) the roba (*Cirrhina roba*), the carmatic carp (*Barbus carmaticus*), the mahaseer (*Barbus hexagonolepis*), the sarana (*Barbus sarana*), the common carp (*Cyprinus carpio*), the tench (*Tinca tinca*) and many others that are included in this group. These constitute a large variety of suitable species for cultivation in the ponds, etc.

Fish and Man. Fishes have been important as human food from the time of Paleolithic man. Along with his fossils impressions of fish bones have been found. The world fisheries take 35 billion pounds worth annually and employ thousands of persons. In an orthodox country like India, the per capita consumption of fish is estimated to be about 3.9 lbs. Fish is a very popular item of diet in West Bengal where the per capita consumption is 9.38 lbs. The food value of the flesh of fish is great. It contains 13 to 20 per cent of protein and has a good value of 300 to 1,600 calories per pound depending upon the oil content. In most fishes the flesh is white (or reddish) and flaky in texture. Fishes must be consumed or preserved soon after catching as they deteriorate rapidly. There are many different methods of preservation, the simplest being drying and smoking used by even villagers. The modernised method of preservation is canning.

In these days, when vitamins are considered a panacea, fish oils are valued as sources of medicines. Fish oils especially cod-liver oil are being extracted in Bombay. The average Indian diet is deficient in vegetables and fruits, i.e., in vitamins. The cod-liver oil is a rich source of vitamin A and D, it contains on an average about 1000 international units of vitamin A per gram. The shark-liver oil is relatively very rich.

Fish oils are also used for the manufacture of insecticidal soap and chamois leather. It is also used for softening of hides, for steel-tempering and after hydrogenation for the preparation of edible fats. Fish scraps and unmarketable types are transformed into fish meal, an excellent additional protein food for poultry and other farm animals. Fertilizers rich in nitrogen and phosphorus are made from unwholesome fish as well as from fish offal. The total quantity of fish used as a fertilizer or manure is estimated at 9.36 lakhs maunds or 6.6 percent of the annual production. The fish scales, when carbonized produce animal charcoal used for colouring and purifying liquids and solutions. The scales of fish contain an iridescent substance called *guanine* which is used in the manufacture of "pearl essence", used for making artificial pearls. The air-bladder of fish is used in the manufacture of an organic substance *isinglass* which is used for clearing wines, as an adhesive in the preparation of plaster or special cements. It is also used in confectionaries for the preparation of sweet drops. Better quality of *isinglass* is produced by the sturgeon. From the fish guts certain enzymes are extracted that are used in leather industry.

From India large amount of preserved fish is exported to Sri Lanka, Burma and other countries in the Far East. The earning of this export trade is estimated to be over Rs. 298 lakhs per year. Over 8,000 maunds of shark fins are exported to the countries in the Far East. Fish manures estimated at about 1.18 lakhs maunds are exported to Sri Lanka.

Fossil History. The history of fishes is older than that of any vertebrate. It begins some 330 million years ago. The first traces of fishes are found in the form of tiny conical teeth in the Lower Silurian beds of Russia. Some skin plates of the same period have been dug out in the United States of America. The Upper Silurian deposits of the Ludlow "Bone-bed" has provided better fossils, in fact the bed is full of fish bones and spines. Fishes developed considerably during the Devonian time in which their fossils are abundant. The fishes of this period contain fossils of the shark, sturgeon and lungfish groups and also armoured ostracoderms and placoderms. The development and evolution of fishes continued in the Carboniferous and Permian times when more and more fishes left the shallow waters near the shore and took to the deep sea. In the Rhaetic beds near Penarth many fish bones were found together with the teeth of a lungfish very similar to the species found even now in Australia. In the Portland stone of Jurassic occurred fishes that form a connecting-link with the true bony fishes or Teleostei. In the Chalk hills of Cretaceous times also bony fish fossils are numerous, evidently they flourished in that period and apparently replaced those of the sturgeon group. The bony fishes were dominant some 70 million years ago and in the Oligocene their development increased further. The bony fish in the modern times represent the great majority of fishes, those of the sturgeon group (ganoids) are reduced to a mere handful of species and the lungfishes (Dipnoi) are reduced even more.

CLASSIFICATION

The class *Osteichthyes* (Teleostomi) includes the vast majority of fishes. They are forms in which a bony skeleton persists. In the skull, jaws, gill-coverings and in a set of bony scales of the body there is a common characteristic pattern, with slight variations of course, in most members of the group. It was formerly believed that these fishes were descendants of shark-like forms and that bone was a new acquisition. But further investigations make it more likely that the bony skeleton is older. The bony skeleton of ostracoderms and placoderms has been retained and perfected forming the skeleton of the true bony fish. The first bony fish appeared in the early Devonian and they have existed up to the recent times. About 95 per cent or more of all fishes are members of this class which contains more than 25,000 species.

The following are the general characters of the class:— skull usually hyostylic; endocranium more or less ossified; palatoquadrate not fused with the endocranium; a single external gill-opening covered with operculum supported by special skeleton of opercular bones, branchial septa reduced, supported by double row of branchial rays; otoliths solid; as a rule an air-bladder or lung is present. Occur from Devonian to Recent.

The class Osteichthyes (Teleostomi) is divided into two subclasses: (A) *Crossopterygii*; (B) *Actinopterygii*.

Subclass CROSSOPTERYGII

The Teleostomi that include many fossil forms among which are the ancestors of the land vertebrates. This subclass is represented by only one living genus *Latimeria*. They first appear in Devonian (about 350 million years ago), and their fossil record ceases 70 million years ago. The following are the general characters of the class: paired fins with a scale covered lobe containing radials; skeleton of the pectoral fin with a jointed central axis bearing radials on each side; a squamosal traversed by the jugal sensory canal; clavicle is present; two dorsal fins, caudal fin, diphyccercal (or of types described as gephyrocercal, heterodiphyccercal, or heterocercal), internal nares (choanae) present; endocranium usually divided in the region of the foramen of the fifth nerve into two pairs, an anterior and a posterior, movable on each other; a hinge between parietals and frontals corresponding to an unossified region which separates the basisphenoid and basioccipital. Almost all are fresh water forms. Occur from Devonian to Recent.

The subclass is divided into two superorders. *Osteolepides* (Rhipidistia) and *Coelacanthi*.

Superorder Osteolepides. The *Crossopterygii* in which the caudal fin is heterocercal or diphyccercal, never consisting of three lobes, a subopercular ectopterygoid is well developed, and scales are with an outer layer of cosmine. Occur from Lower Devonian to the upper Carboniferous. This superorder is divided into the following three orders.

*Order 1. *Osteolepiformes*. The *Osteolepides* in which the scales are rhombic, the paired fins are with a short rounded lobe and endocranium is ossified into two pieces, an anterior and a posterior. From Middle Devonian to Upper Carboniferous.

Example: **Osteolepis*.

*Order 2. *Holoptychiiformes*. The *Osteolepides* in which the scales are cycloid, no vertebral centra are present, and the paired fins are provided with long acute lobes. Occur in Middle and Upper Devonian.

*Order 3. *Rhizodontiformes*. The *Osteolepides* in which the scales are cycloid and thin, ring vertebrae sometimes present and paired fins with a short rounded lobe. Occur from the Middle Devonian to Middle Carboniferous.

Examples: **Rhizodus*, **Strepsodus*, **Eusthenopteron*.

Superorder Coelacanthi. The *Crossopterygii* in which the caudal fin is diphyccercal consisting of three lobes, in the upper and lower lobe each fin-ray corresponding to a single radial; no subopercular (if present very feebly developed); ectopterygoid

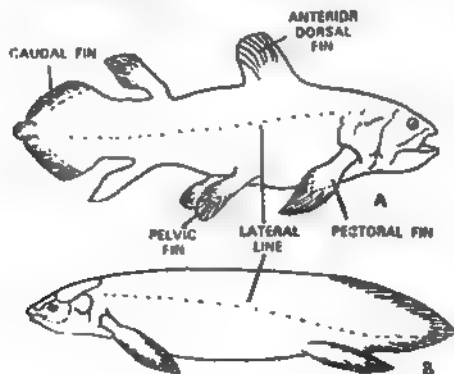


Fig. 4.32. A, *Latimeria*; B, *Neoceratodus*.

reduced; air-bladder ossified hyomandibular reduced; not ossified and taking no part in supporting the lower jaw. The superorder has only one order, Coelacanthiformes.

Order Coelacanthiformes. The Coelacanthi in which the scale is cycloid, thin, no vertebral centra are present except in the caudal region of some forms. Occur from the Upper Devonian to Recent.

Example: **Coelacanthus*, **Rhabdoderma*, **Diplocercides*, *Latimeria* (living).

Subclass ACTINOPTERYGII

The Teleostomi that include all common fish except sharks and skates and are characterized by bony skeleton (hence Osteichthyes). There is an absence of a central axis in paired fins, no opening of nostrils into the mouth and the scales are ganoid (not cosmoid). A jugal sensory canal is lacking and the primitive forms possess only a single dorsal fin. They appear first in the Devonian (about 300 million years ago). Originally fresh-water forms but later colonized in the sea.

This subclass is usually divided into three groups Chondrostei, Holosteï and Teleosteï (Stensio, 1932). Regan divided it into two, Palaeopterygii corresponding to Chondrostei and Neopterygii (corresponding to Holosteï+Teleosteï). Further work of some authors (Stensio) has shown that the Chondrostei gradually merge in Holosteï and that they can be separated from the remaining orders only artificially. Likewise, the difference between Holosteï and Teleosteï is not very distinctive and the two groups gradually merge. It is not possible to draw a sharp line of distinction between the Chondrostei and Holosteï, and Holosteï and Teleosteï. It is better, therefore, not to divide the Actinopterygii into these controversial groups (Chondrostei, Holosteï and Teleosteï), but to classify it into a series of orders.

The whole subclass is divided into two groups which have been classified into about 60 orders. Here a description of only the important ones is given.

Group A. This group has been separated to accommodate the Polypteriformes which differ from all the Actinopterygii in the structure of the pectoral endoskeleton and of the dorsal fin.

Order Polypteriformes. The Actinopterygii with scales, typical rhombic, ganoid and provided externally with small denticles. Caudal fin symmetrical, although not typically diphyccercal, dorsal fin with many peculiar fin-lets, pectoral fin with a small prominent base covered with scales, vertebral column well ossified, no choanae, dorsal and ventral ribs present; air-bladder bilobed, cellular opening into the intestine ventrally.

Formerly this order was placed in the Crossopterygii (Huxley and Woodward) but as is obvious from the above characters there are no grounds for doing so.

Polypterus the bichir of African rivers, is one of the two living genera of this group, the other being *Calamochthys* also found in rivers of Africa. *Polypterus* shows many ancient characters, rhomboidal scales hardly overlapping; the presence of a spiracle, the arrangement of the skull bones. In the intestine there is a spiral valve; there is a single pyloric caecum and the tail is no longer markedly heterocercal but shows distinct signs of that condition.

Group B. The Actinopterygii in which the pectoral radials attached at least partly, immediately to the scapulo-coracoid cartilage or the scapula and coracoid. This group includes the following 59 orders according to Berg.

- | | |
|-------------------------|--------------------------|
| 1. Tarraiiiformes | 9. Ospiiformes |
| 2. Palaeonisciformes | 10. Pholidopleurniformes |
| 3. Gymnonisciformes | 11. Saurichthyiformes |
| 4. Phanerorhynchiformes | 12. Acipenseriformes |
| 5. Dorypteryniformes | 13. Amiiformes |
| 6. Bobasatraniformes | 14. Aspidorhynchiformes |
| 7. Redfieldiiformes | 15. Pyenodontiiformes |
| 8. Perlebiidiformes | 16. Pachycormiformes |

¹ Sometimes regarded a class of fish, here it is classified as a subclass of Teleostomi (Osteichthyes).

- | | |
|-------------------------|--------------------------|
| 17. Lepidosteiformes | 39. Percopsiformes |
| 18. Pholidophoriformes | 40. Stephanoberyciformes |
| 19. Clupeiformes | 41. Beryciformes |
| 20. Bathyclupeiformes | 42. Zeiformes |
| 21. Glaxiiformes | 43. Mgiliformes |
| 22. Scopeliformes | 44. Polynemiformes |
| 23. Ateleopiformes | 45. Ophiocephaliformes |
| 24. Giganturiformes | 46. Symbranchiformes |
| 25. Saccopharyngiformes | 47. Perciformes |
| 26. Mormyriiformes | 48. Dactylopteriformes |
| 27. Cypriniformes | 49. Thunniformes |
| 28. Anguilliformes | 50. Pleuronectiformes |
| 29. Haliosauriformes | 51. Icosteiformes |
| 30. Notacanthiformes | 52. Chaudhuriiformes |
| 31. Beloniformes | 53. Mastacembeliformes |
| 32. Gadiformes | 54. Echeineiformes |
| 33. Macruriformes | 55. Tetradontiformes |
| 34. Gasterosteiformes | 56. Gobiesociformes |
| 35. Syngnathiformes | 57. Batrachoidiformes |
| 36. Lampridiformes | 58. Lophiiformes |
| 37. Cyprinodontiformes | 59. Pegasiformes |
| 38. Phallostethiformes | |

*Order **Palaeonisciformes**.¹ Maxillary hardly movable, firmly united with the ectopterygoid; caudal fin heterocercal, no interoperculum notochord persistent; scales ganoid; single dorsal fin. From middle Devonian to lower Cretaceous.

Examples: **Chairolepis*, **Canobius*, **Stegotrachelus*.

Order **Acipenseriformes**. Snout elongated, body covered with five rows of bony scutes or naked, caudal fin heterocercal; endocranium cartilaginous overlaid by few bony shingles, never ossifying as a complete box; there is an open spiracle. Lower Lias to Recent.

Examples include *Polyodon*, the paddle fish of the Mississippi and Chinese rivers and *Acipenser* and other modern sturgeons occurring both in the sea and fresh water.

Order **Amiliformes** (Protospondyli *ex parte*). Caudal fin abbreviate heterocercal; premaxillae firmly articulate with cranium; interopercular present; several pectoral radials inserted on metapterygium upper Permian to Recent.

BONY SCUTES

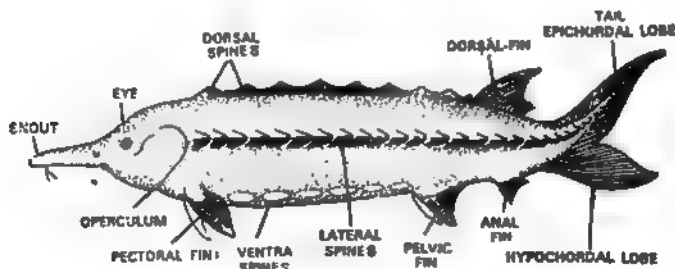


Fig. 433. *Acipenser*

¹ What is here treated as an order is usually regarded as a simple family by Stensi (1932), however, others are inclined to divide it into several families.

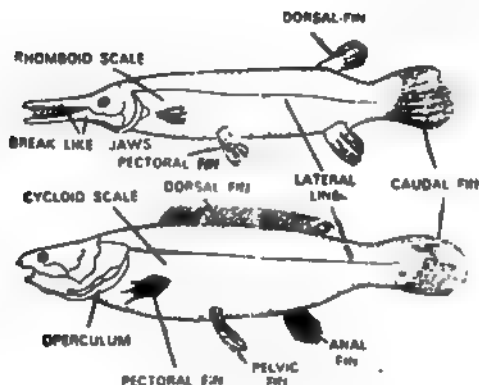


Fig. 4.34. A, the garpike *Lepisosteus*; B, the bowfin, *Ameiurus*.

Examples: *Ameiurus*, the bowfin, **Sinamia*

Order **Lepidosteiformes** (Ginglymodi). Nasal opening at the end of the much elongate snout, all fins with biserial fulcra; head bones covered with ganoin; caudal fin abbreviate heterocercal, air bladder cellular. Upper Cretaceous to Recent.

Example: *Lepisosteus*, the gar-pike.

Order **Clupeiformes** (Isopondyli or Malacopterygii). Caudal fin homocercal, no fulcra; vertebral centra usually completely ossified no Weberian apparatus; upper jaw usually bordered by premaxillae; traces of ganoin only in fossils, scales usually cycloid. This order from which a series of higher orders have arisen, represents an artificial assemblage. Middle Triassic to Recent.

Examples: *Hilsa ilisha* (family Clupeidae; herrings); *Chirocentrus* (family Chirocentridae); *Salmon* (fam. Salmonidae); *Esox* (fam. Esocidae); *Notopterus* (fam. Notopteridae; feather backs); *Leptolepis* (fam. Leptolepidae).

Esox (the pike) is a carnivorous fish of predaceous habits, unsurpassed in greediness and voracity. *Gastrosteus* (sticklebacks) are remarkable for the perfect indifference with which they can be transported from fresh into salt water and vice versa, and for the elaborate nests which the males build in fresh brackish water. They watch the eggs deposited by the female.

Order **Cypriniformes** (Ostariophysi or Plectospondyli). A peculiar Weberian apparatus connecting the ear with air-bladder is present; air-bladder, as a rule, connected with a duct to the elementary canal; ventral fins, if present, abdominal, first appeared in Cretaceous. This is a vast order of fishes inhabiting fresh water and is divided into two divisions.

Division Cyprinae—Carps.

Examples: *Labeo*, *Cirrhina*, *Barbus*, *Carrasius*, the gold fish (all family Cyprinidae).

Division Siluriformes—Cat-fishes.

Examples: *Wallago* (Siluridae); *Heteropneustes* (Saccobranchius); fam. Heteropneustidae; *Clarias* (fam. Clariidae); *Mystus* (fam. Bagridae).

Order **Anguilliformes**. Body eel-like; air-bladder, if present, connected with intestine by a duct; scales, if present, cycloid; no separate premaxillae; dorsal and anal fins very long confluent behind. Upper Cretaceous to Recent.

Examples: *Anguilla* (fam. Anguillidae) famous for migratory power; *Moringus* (fam. Moringuidae); *Ophichthys* (fam. Ophichthyidae).

Order **Bloniformes**. Physoclistic fishes in which fins are without spines; ventral fins abdominal; pectorals inserted high up scales cycloid; lateral-line running very low Eocene to Recent.

Examples: *Belone* (= *Xenanthodus*; fam. Belonidae); *Exocoetus* (fam. Exocoetidae).

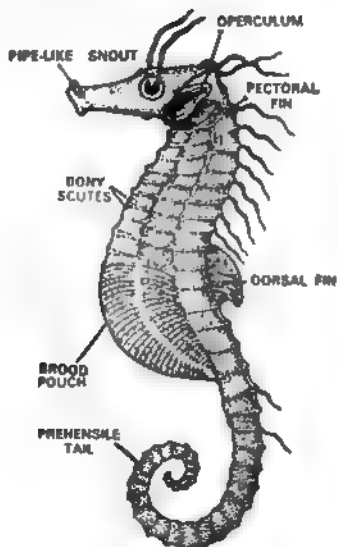


Fig. 4.35. The sea-horse *Hippocampus*.

Exocoetus, the flying fish that makes great leaps out of water and actually sails through the air. The pectorals in this are developed to form swallow-like wings (Fig. 4.38) and are used as parachutes.

Order Syngnathiformes. Physoclistic fishes in which the first dorsal fin, if present, is spinous; ventral fins, if present, abdominal or subabdominal, mouth terminal bordered by premaxillae or both premaxillae and maxillae; snout tubiform.

Examples: *Hippocampus* (sea-horse), *Syngnathus* (both fam. Syngnathidae).

Syngnathus (pipe-fishes). Snout produced; mouth small and at the tip of the snout. Skin with bony plates arranged in rings, gill-openings very small and near the upper posterior angle of the gill cover; one soft dorsal fin; pelvics absent, males with an egg-pouch placed on the ventral side of the abdomen, usually formed of two folds of skin; eggs retained here till some time after hatching; tail prehensile and with a caudal fin. *Hippocampus*, the sea-horse swims with the body in a vertical position. In most species the male takes charge of the eggs in a pouch under the tail, in a groove under the tail or under the abdomen. The tail is prehensile without caudal fin, other features agree with those of *Syngnathus*.

Order Symbranchiformes. Eel-like body; no air-bladder; no spines in fins; dorsal, caudal and anal fins continuous; branchial openings joined in a single transverse central slit, gills usually reduced; respiration chiefly buccopharyngeal and intestinal.

Example: *Amphipnous* (fam. Amphipnoidae). *Amphipnous cuchis* (cuchia) is an inhabitant of fresh and brackish waters of India and Burma, growing to two feet in length, remarkable for the presence of a respiratory air sac, on each side of the head, communicating with the gill-cavity.

Order Perciformes (Acanthopterygii). Physoclistic fishes with fins usually with spines; usually two dorsal fins, the first normal; maxillae usually quite excluded from the gape. Uppermost Cretaceous to Recent. It is a vast order of marine fishes.

Examples: *Ditrema* (fam. Embiotocidae); *Fierasfer* (fam. Fierasferidae), *Anabas*, the climbing perch (fam. Anabantidae).

Fierasfer is without pelvic fins; vent at the throat, eel-like small shore-fishes of

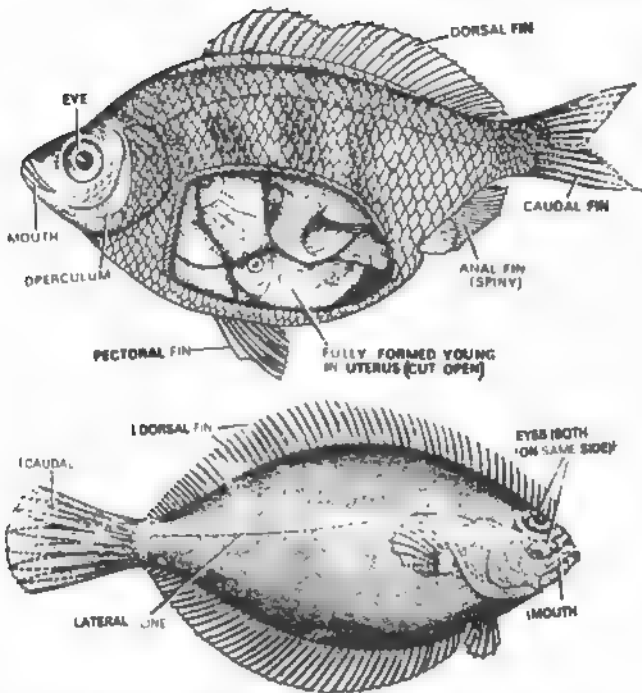


Fig. 4.36. A, a viviparous fish (*Cymatogaster aggregata*) whose uterus has been cut open to show the embryos; B, the flatfish (*Hippoglossoides platessoides*).

tropical seas often living as lodgers in the cavities of holothurians, star-fishes and bivalve molluscs, often commensal with the pearl oyster

Order Dactylopteriformes. Physoclistic fishes in which fins are usually with spines; nasals fused together forming a single median bone; pectoral radials four rod-like; pectoral fins very large divided into two portions

Examples: *Dactylopterus* (fam. Dactylopteridae).

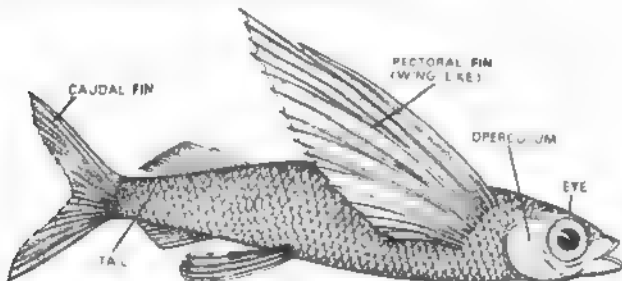


Fig. 4.37. The flying fish *Exocoetis*.

Order Pleuronectiformes. Resembles Perciformes in essential features but both eyes are situated on one side and skull is asymmetrical; fins usually without spine; adults without air-bladder.

Examples: *Pseudorhombus* (fam. Bothidae); *Cynoglossus* (fam. Cynoglossidae); *Solea* (fam. Soleidae).

Order Echeniiformes. This order also resembles Perciformes in essential features, but the spinuous dorsal fin is transformed into an adhesive disc placed on the head; no spine in second dorsal and anal fin; no air-bladder.

Example: *Echeneis*, (fam. Echeneidae). *Echeneis* is provided a suctorial, transversely laminated oval disc, cephalic sucker, on the upper surface of the head (modified dorsal fin). Pelvics are thoracic. Found in all seas; attach themselves to floating objects and other fishes by means of the cephalic sucker. Used to catch the edible turtles.

Order Ophiocephaliformes. Physoclistic fishes in which the fins are without spine; ventral fins subabdominal; a non-labyrinthic suprabranchial organ (accessory respiratory organ) is present; scales cycloid; air-bladder very long prolonged into the caudal region, bifid posteriorly.

Example: *Channa* (= *Ophiacephalus* family Ophiocephalidae).

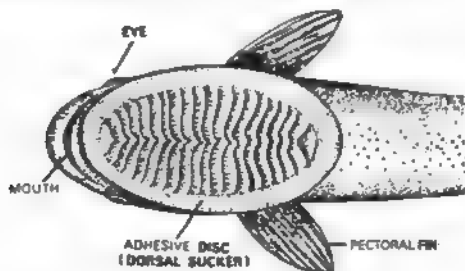


Fig. 4.38. *Echeneis*.

Order Mastacembeliformes. Eel-shaped physoclistic fishes in which the dorsal caudal and anal fins are confluent, some free spines before dorsal fin, no ventral fins; mouth bordered by premaxillae only; branchial openings small, ventral.

Example: *Mastacembelu*, (fam. Mastacembelidae).

Order Tetradontiformes. Gill-openings restricted; ventral fins, if present, thoracic or subthoracic; air-bladder present or absent; air-sacs present or absent. Lower Eocene to Recent.

Examples: *Tetrodon*, *Diodon*, the porcupine fish, (both belong to family Tetradontidae).

Order Gadiformes. Physoclistic fishes in which fins are without spines; ventral fins jugular; scales cycloid; caudal fins of the pseudocaudal type.

Example: *Gadus* (cod; fam. Gadidae).

CLASS DIPNOI

The Dipnoi are specialised fishes with gills, lungs, external and internal nares and reduced scales. Skull is cartilaginous and covered with a few large scutes. Jaws are short autostylic with teeth in the form of crushing plates. There are no vertebrae in the modern Dipnoi, the notochord is persistent as an unsegmented rod. An operculum covering the gill is present. Paired fins are with unsegmented cartilaginous axes and caudal fin is diphycercal. The air-bladder develops into a definite lung-like structure

¹ In most text books Dipnoi has been described as a subclass of the class Choanichthyes or superorder of the subclass Choanichthyes. But here it has been raised to the status of a class following the classification of Berg (1947).

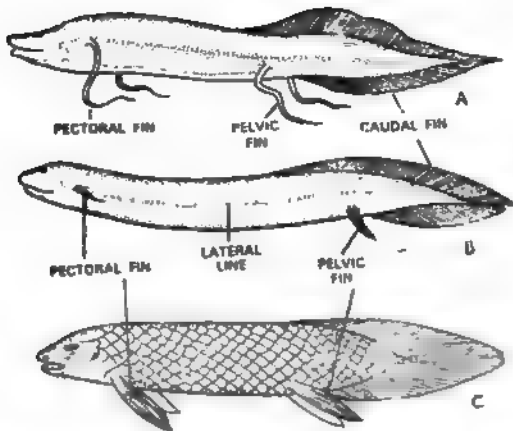


Fig. 4.39. Lungfishes. A, *Protopterus*, the African lungfish, adult about 32 inches long. B, *Lepidosiren*, the South American lungfish, adult about 32 inches long. C, *Neoceratodus*, the Australian lungfish the adult of which attains a length of 40 inches.

(one in *Neoceratodus* and two in others) which form very efficient respiratory organ. Vascular system and heart are well developed, on the amphibian plan, and deal efficiently with pulmonary respiration. The nervous system shows the amphibian plan. The urinogenital system is also similar to amphibians. The embryonic development and the larvae show distinct similarity to those of the amphibia (especially the larvae of *Lepidosiren* and *Protopterus*).

They are all inhabitants of fresh water and breathe air. Three living genera are known. Of these *Neoceratodus* lives in pool, which becomes low and stagnant, in Queensland. *Lepidosiren* occurs in tropical and South America and *Protopterus* in tropical Africa. When the streams dry up in hot season they burrow deep in the mud and spend the time in a state of lowered metabolism (aestivation). In this state they can remain at least for six months. The moist walls of the burrows keep them from drying out, and a small opening brings air in for respiration. Their food consists of small invertebrates and decaying vegetable matter which is consumed in large amount. They occur from Devonian to Recent.

It is apparent from the above that in many anatomical features and in the mode of development the lungfishes and frog show almost identical conditions. But there are certain specialisations which show that they are off the direct line. The lungfishes, as such, are not ancestors of the terrestrial forms but are closely related with the

5. Class Amphibia

The class Amphibia (Gr. *amphi*, dual+*bios*, life) includes animals that partly live on land and partly in fresh water. The amphibians are the first chordates that lived out of water way back in the Carboniferous, some 275-225 million years ago. The name Amphibia was given to the group by Linnaeus. The group includes such familiar animals as the frogs and toads (*Anura*), the newts and salamanders (*Urodela*) and tropical burrowing legless amphibians (*Apoda*). This is the smallest class of the vertebrates having nearly 2,500 species as compared to 6,000 species of reptiles and more than 25,000 species of bony fishes only. The Amphibia occupy an intermediate place between the fish and reptiles. They have descended from fish-like ancestors, on the one hand, and are themselves ancestors of reptiles that have given rise to the birds and mammals.

The living Amphibia (also called *Batrachia*) are cold-blooded vertebrates possessing four pentadactyle limbs supported by girdles instead of paired fins of the fish, the apodans being without legs. Any median fins are not supported by rays. The skin is soft, glandular and moist lacking in the protective external scales, hair or feathers of higher vertebrates. There are two nostrils that are connected with the buccal cavity. The skull is provided with two occipital condyles. The heart is three-chambered. These animals breathe by gills, lungs and skin. The eardrum is external and is connected by a rod of bone, *columella aurs*, to the inner ear. *Columella* crosses the middle ear. They differ from reptiles in that fertilization is not accomplished by coition, and the eggs are unprotected by a shell and embryonic membranes. Consequently most Amphibia have to become temporarily aquatic for the purpose of reproduction. Modern amphibians have diverged far from those which were ancestral to the reptiles, losing much of their bony skeleton.

EMERGENCE OF AMPHIBIA

The amphibian organization has emerged out of the piscine (fish-like) pattern is almost an established fact. The morphological changes during metamorphosis and the anatomy and palaeontology of both forms furnish evidence to this. The stages in the metamorphosis parallel the stages through which, in phylogeny (evolutionary history), the descent from piscine ancestor took place. The anatomical resemblances between fishes and amphibians is so close that it led Huxley to put both Amphibia and fishes under *Ichthyopsida*. Moreover, the recent researches in Palaeontology¹ leave no doubt that the Amphibia have originated from some fish-like ancestor.

In an attempt to explore the likely fish-like ancestor of the Amphibia it must be borne in mind that the modern Amphibia cannot be compared with the modern fish, because the modern forms have become highly specialized in response to the demands of modern environments. The result of this specialization is that almost all the phylogenetic relationships have been covered up. This, moreover, is a fact that the amphibians have not descended from the modern fish.

In the Carboniferous age there were three distinct orders of Amphibia, as revealed by the fossil history. These included *Labyrinthodontia*, *Lepospondyli* and *Phyllo-*

¹ Dollo, Gregory (1915), Watson (1917, 1919, 1926), White, Williston (1925), Siemss, etc.

spondyli. The first two were present not only in abundance, but presented a variety of forms, in the lower Carboniferous, which indicates that they must have originated earlier, at least, in the Devonian and possibly in the Silurian times.

Another important point that limits our search for the tetrapod ancestor is the fact that the amphibians arose from ancestors in the fresh water, because all the fossil record that establishes the relationship is obtained from the fresh-water deposits. It further reveals that in the Devonian the fresh water-fishes comprised the ganoids (in the broad sense), the dipnoans (lung-fishes) or aberrant-sharks. The ancestor of amphibians must be one of these.

At the first thought it strikes that the dipnoans were the ancestors of Amphibia. This is because of certain obvious resemblances between the modern amphibians such as the urodeles and the modern dipnoans. Both breathe, to a large extent, by lungs and the distribution of blood vessels to and from these organs have close resemblance. Other similarities may be found in certain features of the skull the brain, the urogenital system and early development. Such similarities led some authors to conclude that the urodeles originated from the Dipnoi. The most primitive dipnoan, those from the middle Devonian, may have possessed some of the urodele resemblances mentioned above, but they also possessed a number of distinctive features which would preclude them from the direct ancestorship of the modern Amphibia. A study of the development of the skull (de Beer '37) and of ancestral stocks of the Dipnoi and Amphibia as fossils supports this view, i.e., the amphibians have not originated from the Dipnoi, and whatever similarities exist are due to convergence.¹ In such respects as teeth and skull structure the Dipnoi is definitely on an evolutionary side-line and cannot be considered as ancestor of Amphibia.

This leaves only the ganoids among which to find the ancestors of the amphibians, since the sharks are obviously off the main line of ascent. Among these the Actinopterygii, one of the major subdivisions of the group, do not come close to the ancestral position because of the absence of internal nostrils and lack of a large fleshy fin from which a land-limb might develop. This diverts the attention to the other subdivision of fishes, i.e., the Crossopterygii or the lobe-finned fishes. One family of the Devonian crossopterygians called the Osteolepidae agrees so closely with the primitive Amphibia (i.e. Embolomeri, an extinct suborder of the Labyrinthodontia), in most important skeletal features that there can be no doubt that the amphibians branch off from a fish very closely allied to this family, and in all probability from the genus *Eusthenopteron* of Rhizodontidae (Swinton, 1953).

Whatever may be the stem-fishes that gave rise to amphibians, it is certain that the emergence of the Amphibia was very slow and gradual, not as sudden and revolutionary as reflected by the metamorphosis of the modern forms. Keeping in view the Devonian conditions it has been suggested that the ancestral Amphibia made their appearance on land in their attempt for remaining in water. During seasonal droughts the water dried up from some ponds and the ancestors of amphibians with their short, clumsy but effective limbs attempted to crawl out of the drying pool and walk overland to reach the next pool where water still remained. Thus the 'land-limbs' as held by Romer (1947), were developed to reach water and not to 'leave it'. Apparently they seem to have been aquatic forms in the beginning, but owing to abundance of insects they might linger on banks to prey upon them and thus tended to become terrestrial, which they could do during the Carboniferous and Permian time.

The primitive Amphibia as represented by the Embolomeri and their allies presumably departed but slightly from the crossopterygian ancestors of the Amphibia. They were decidedly fish-like in most of their skeletal anatomy although they were definitely on the Amphibian side of the boundary. In the only forms in which the skeleton is at all known, the body was much elongated, with a powerful tail but small limbs. Such Embolomeri were, probably, persistent water-dwelling fish-eaters. It may as well be pictured that the first Amphibia such as *Eogyrinus*, *Palaeogyrinus*, swimming alongside their cross-opterygian ancestors and differed from the latter

¹ Animals of dissimilar or unrelated groups develop similar characters (parallelism) as they have to lead life under similar environmental conditions.

mainly in having feet instead of fins. In fact, amphibia were prepared for life on land before they were forced into the terrestrial world. Still it is probable that a need for terrestrial adaptations existed at the time the Amphibia were evolving.

Once this process had begun all those changes in the body organisation started setting in, that were needed by the fish ancestor to grow into modern Amphibia. All these changes involved features for the adaptation of life on land such as a change of gill to lung and associated double flow of the blood into the heart and elaborate development of the organs of sense, the auditory, optic and olfactory. The Amphibia reached the peak of their career during the upper Carboniferous and Permian periods, and then dwindled, doubtlessly unable to compete with much better equipped descendants and rivals on the land, the Reptiles.

TYPE FROG

The frog, although highly specialized amphibian, is usually described as a type of the class, because the frog is easily obtained. It is a nice, clean animal easy to dissect, and is admirably suitable for physiological experimentations. The frog has been a favourite object of study for a long time. No other animal except man has been the object of so many observations as the frog. The frog generally lives in or near water but wanders away from the aquatic home in damp or wet weather. It is obligatory for the frog to live near water because in order to breathe by skin it has to be kept moist, because the eggs are laid in water in which the young hatch out and lead an aquatic life some time, and because water affords a good means of protection to these defenceless animals.

The frog produces croaking sound in rainy season. The voice of the male is hoarser, deeper and louder and is used as a call to the mate. Female croaks are slower and rarer. Frogs also utter a pain scream when attacked by enemies. When caught in hand it makes violent efforts to escape using its fore- as well as the hind limbs. At the same time a fluid is poured out to make the already slimy skin more slippery. It also inflates its lungs which aid slipping. The frog is a "cold blooded" animal, i.e., its temperature varies with that of the environment. It cannot, therefore, bear frost or intense cold or even intense heat.

During intense cold the frogs bury themselves deep into the mud and take rest. This phenomenon is known as **hibernation** or **winter sleep**, during which lung breathing is stopped, skin-breathing continues, and the frogs consume energies stored in their bodies. They remain inside till the rain falls. The frogs breed in the rainy season, appearing with the first shower. The eggs are laid in water and after the egg laying the parents pay no attention to them, but lead a carefree life of excessive feeding. The development depends upon the environmental conditions. In shallow ponds the frogs hatch earlier because they get warmer soon. In deeper waters hatching may take long. During breeding time a number of frogs gather together at certain places in shallow water. After discharging the sexual products they scatter on the grounds.

The frogs do not drink water but absorb it through the skin which is loosely attached to the body and, as such, is able to store considerable amount of water. It has also been observed that the outer layer of skin, which consists of a very thin transparent membrane, is cast off at certain periods. The cast skin comes off in large patches usually the skin covering the toes comes out last. The frogs usually eat the shed skin.

Locomotion. The locomotion in the frog is brought about in two ways. (i) by **leaping**, and (ii) by **swimming**. In ordinary resting position the front part that is inclined upwards is supported by fore-limbs having a peculiar twist. The posterior part of the body is supported on the hind legs, folded as if ready for a spring. From such a sitting or **squatting posture** it jumps by a sudden extension of the hind-limbs. The fore-limbs are used to hold up the anterior part of the body and to manipulate the direction, for which it adjusts its body in a new direction before each leap. An ordinary frog can jump from two to three feet in each leap. In swimming also the hind-limbs are used. In the starting position the hindlimbs are folded in the manner of letter Z (as in leaping), but as the animal begins to swim the legs are extended quickly. As the hind-limbs are long and the toes are webbed they act like oars enabling the animals to swim. The fore-limbs are held back after each stroke and if the animal does not make

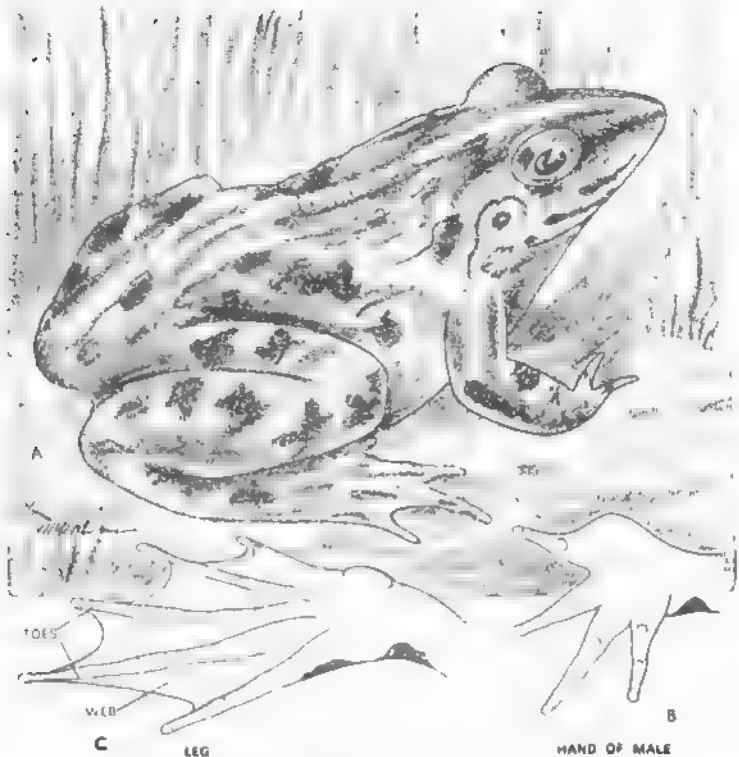


Fig. 5.1. A, Frog in a sitting posture; B, Hand of male; C, Leg of male.

strokes in succession the hind-limbs and the body are kept in straight line. The fore-limbs serve two purposes, they help in propelling the animal to some extent and in guiding the direction of movement.

External Characters. The body of the frog is divided into two parts, the head and trunk. A tail is lacking in the adult condition and there is no neck. The head is almost triangular in shape joined directly to the trunk, as the neck is absent. The head bears two large prominent eyes one on each side of the head. The eyes are round and bulging. When pressed downwards they make marked prominence in the buccal cavity. The eyes do not rest on any bone as in the higher animals. The eyes are protected by two eyelids, the upper eyelid is thick pigmented and capable of small movements, but the lower one is thin semi-transparent and capable of free movement. Each time the frog closes the eyes they are pressed downwards. In the eye of the frog also a **nictitating membrane** is present. It lies just above the lower eyelid from which it is separated by a groove. It is relatively more transparent than the lower lid. The pupil is a dark oval opening. Behind the eye, on either side, there is a nearly circular obliquely placed area covered by a tough membrane, the **tympanic membrane**. A careful observation reveals a small prominence in the centre of the tympanic membrane. This is caused by **columella**, the bony rod that lies inside.

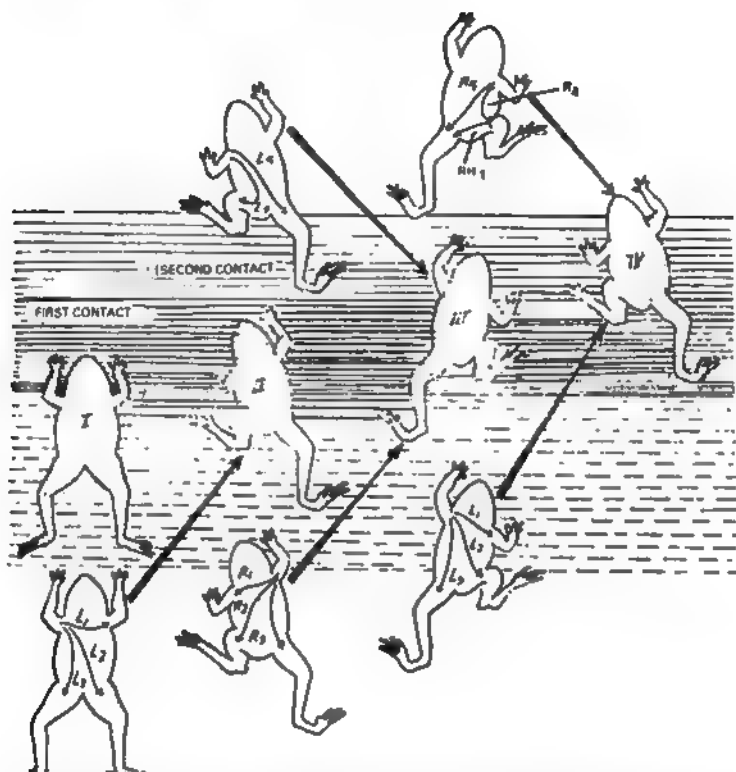


Fig. 5.2. Reflexes associated with the transition from swimming to walking in toads. The shaded outlines show successive positions as the animal emerges on the solid ground. The first effective contact is by the left fore limbs whose reactions and extension elicits a crossed protection reflex in the right fore-limb (L1) a diagonal extensor response in the right hind-limb (L2), and a placing response in the left hind limb (L3). The right fore-limb touches the ground and reduces corresponding responses (R 1—2). The left fore-limb swings forward in response to stretch of its protractor muscles, producing retraction of the left hind-limb (L4) and protraction of the right hind-limb (L5). Then the fixation of the right hind foot produces a crossed flexor response (RH-1) (after Gray).

Among the external apertures the **mouth** is a wide horizontal opening into the buccal cavity and extending nearly from one ear to the other. At the posterior end of the body between the two legs is situated the opening of the **cloacal aperture**. Lying above and behind the tip of the snout there are two **external nares** or the nostrils. Each narial opening is guarded by a valve externally, leads into the buccal cavity opening at the **internal nares**.

The trunk bears two pairs of limbs. The **fore-limbs** are short bearing four fingers and an inconspicuous thumb which can be felt within the skin. The **hind-limbs** are longer, admirably adapted for jumping and swimming. The foot of the frog has five webbed toes.

Skin. The skin of the frog is smooth (has no scales or hairs etc.), moist and is loosely

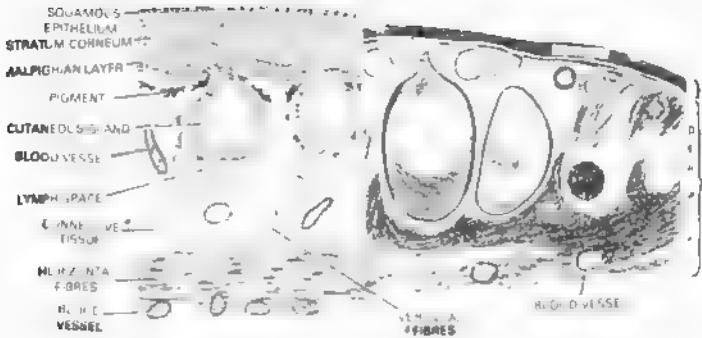


Fig. 5.3. Vertical section of the skin of the frog.

attached to the body. Large subcutaneous lymph spaces separate the skin from the body wall. The skin is thicker on the dorsal side of the body than that on the ventral. It is composed of two layers, the **epidermis** and **dermis**. The epidermis is composed of several layers of cells and is renewed at interval by a process of moulting. The outer layers of the epidermis are heavily cornified, this is a typical character of land vertebrates. The moult is controlled by the pituitary and thyroid glands and does not occur if either of these is removed. In such cases the keratinized cells keep on merely accumulating as a thick skin. Local thickening of the epidermis often occur in Amphibia, for instance, to form horny teeth by which the larva feeds. Such papillae are also a conspicuous feature of warty skin of toads (*Bufo*). These local thickenings suggest the origin of feathers and hairs. The cells of the innermost layer of epidermis are columnar (**stratum germinativum**). The cells of this layer are capable of multiplying as new cells are produced they pass towards the outer surface and become more and more flattened as they reach the surface. The cells of the surface (**stratum corneum**) become broad and thin.

The epidermis, especially on the dorsal side of the body, usually contains more or less dark brown or black pigment, which occurs partly within special cells, the **chromatophores**, and partly in between the typical cells of the epidermis. In certain regions all the cells of the epidermis may contain all pigment granules. The epidermal pigment appears and disappears in the same region in the course of a few months (Ehrmann). The chromatophores of the epidermis resemble the dark pigment cells of the dermis. The chromatophores of the epidermis are not usually abundant. The main source of colour is located in the pigment cells of the dermis.

The dermis is divisible into two layers, an outer comparatively loose layer (**stratum spongiosum**) containing most of the glands and an inner layer (**stratum compactum**) of dense connective tissue. The stratum spongiosum consists of a loose network of fibrous connective tissue richly supplied with lymph spaces and blood vessels. Just beneath the epidermis it forms a thin layer which contains numerous pigment cells. In the deeper portions are embedded the glands. The stratum compactum comprises dense layer of connective tissue whose fibres run in a wavy course parallel to the surface of the skin. At intervals this layer is crossed by vertical strands, which often extend through the stratum spongiosum into the epidermis. The vertical strands consist of connective tissue fibres and may also contain smooth muscle fibres, elastic fibres, nerves and blood vessels. The fibres aid in squeezing out secretions of the cutaneous glands.

Beneath the stratum compactum lies a loose layer of **sub-cutaneous connective tissue** which is separated by large lymph spaces into two, one beneath the stratum compactum the other above the musculature. At the septa the two layers become continuous. The outer of the two layers is very vascular and contains numerous stellate

cells, within which are numerous grayish white pigment granules. These cells are abundant on the underside of the body, where they produce the white coloration characteristic of the under surface.

Glands. The glands of the skin are more developed in the amphibians than in fishes. There are two types of glands, the **mucous glands** and the **poison glands**. These glands are of the simple alveolar type and lie mainly in the stratum spongiosum of the dermis. Only rarely (as in the large glands of the inner finger) do they extend into the deeper portion of the skin. Typically the glands are spherical or oval in form, and open through the surface through narrow neck which extends through the epidermis and terminates in the triradiate opening at the outer end. The mucous glands are smaller and much more abundant than the poison glands, and are found practically over the entire surface of the body. They are lined with a single layered epithelial cells except near the opening of the neck where there are two layers. The ducts of these glands are narrow, and lined with a layer of small flattened epithelial cells. The mucous serves to keep the skin moist, essential for cutaneous respiration. The mucous also prevents evaporation and maintains the amount of necessary water. Frogs in dry air are always found to be colder than their environment. Evaporation produces large influences of temperature. Thus cooling is also connected with the control of evaporation by mucous and is probably used by animals like the tree-frog (*Hyla*) which are found fully exposed to tropical sunlight which would be expected to raise their temperature to a level dangerous for the life of the animal.

The **poison glands** are larger and less abundant than the mucous glands, and are less uniformly distributed over the surface of the body. They are relatively more numerous on the dorsal side of the body and on the hind legs. The epithelium of the poison glands consists of cylindrical cells filled with granules. The secretion of the poison glands is a whitish fluid with a reported burning taste. Comparatively little is known about the property of the poison in the frog. Paul Bert inoculated a goldfinch with the dermal secretion of *Rana esculenta* and the goldfinch died within one minute. A frog inoculated with the poison of another frog of the same species died within an hour and a quarter. The poison glands are less developed in *Rana* than in *Bufo*, where they are grouped forming **parotid glands**. The effect of the poison on man is to produce an irritation of the eyes and nose only rarely does it affect the skin of the hands. When swallowed it produces nausea and has a digitalis-like action on the heart.

Some amphibians produce certain secretions with characteristic smells. The function of these secretions, perhaps, is to attract the opposite sex. Some male newts (*Plethodontidae*) have special collections of these gland cells below the chin. Another function of the glandular secretion is to keep the eyes and nostrils free from obstructions.

Colour. The colour of the common frog is olive green with dark spots and patches. The hind legs are marked by cross bars of brownish green colour. The ventral surface is yellowish white. The males are usually of a darker colour than the females. The colour is produced by three layers of pigment cells, the **melanophores** lying deepest, the **guanophores** lying next and the yellow **lipophores** overlying these. The guanophores are full of granules which by diffraction produce a blue green colour while the lipophores filter out the blue. The skin of the frog is able to change colour in harmony with the surroundings. This property is at its highest in the tree frog that assumes bright green colour among the green leaves of a tree, when on the bark their skin turns gray or brown. The change in colour is produced by expansion of the pigment in the melanophores under the influence of the secretion of the pituitary gland. Movement in the other chromatophores can also affect the colour, yellow being produced by the disarrangement of guanophores. Blue (though rarely) is produced by the absence of lipophores and red by pigment in lipophores. These colours may contribute to the patterns that the animals present.

As in the bony fishes the pigment cells are not directly controlled by nerve fibres. Therefore the colour change is rather slow. The melanophores show slight changes correlated with change of incident illumination even after the removal of the pituitary. This indicates that the melanophores respond directly to light. Other factors that

influence colour in Amphibia on the whole are temperature and humidity. The colour patterns adopted are usually **cryptic** or **concealing** in their effect. Many frogs suddenly expose brightly coloured patches on the thighs when they jump. This presumably serves to startle the attacker and as such the colours have been called **dynamic** or **startling**. However remarkable the changes in colour a frog may undergo, but none is able to assume all shades and hues. The colour also protects the organs from the effects of light, which may cause contraction when it falls directly upon muscles. Dark colour both in the adults and eggs may also assist in the absorption of heat.

ENDOSKELETON

The skeleton of the larval frog is cartilaginous, but later, in the adult, many parts become bony. Cartilage persists on the ends of limb bones to form smooth joint surfaces and in parts of the skull and limb girdles. The skull, vertebral column and

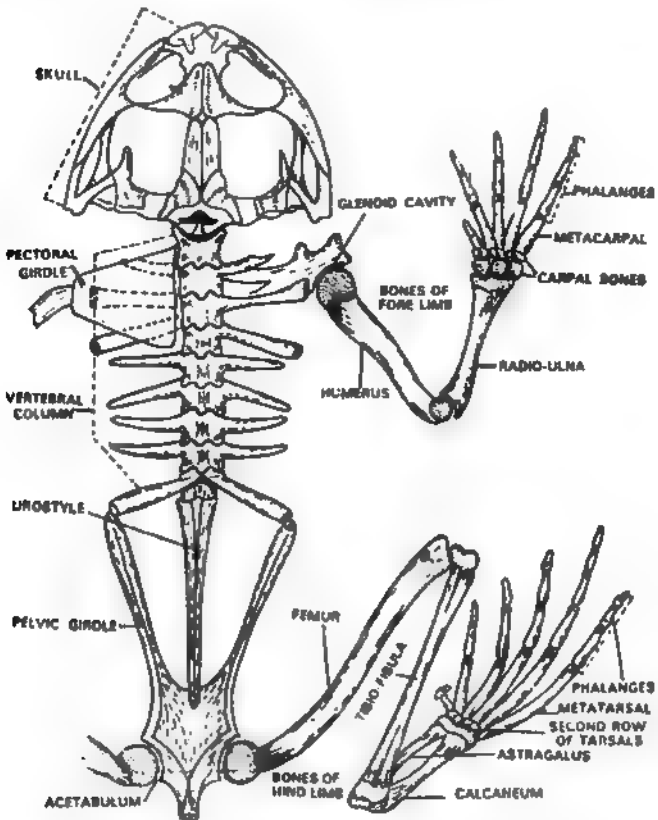


Fig. 5.6. Skeleton of frog (limb bones from one side and a part of shoulder girdle removed).

sternum comprise the axial skeleton and the limbs and umb girdle from the appendicular skeleton.

Skull. The broad flat skull consists of a narrow brain case or cranium, the paired **sense capsules** of the nose and ear and large orbits for the eyes, and the jaws, hyoid and cartilages of the **larynx**. The **cranium** is the narrow cavity lodging the brain. It is cartilaginous in nature being narrowest between the orbits that lodge the eyes. Posteriorly there is a large opening of the cranium through which passes the spinal cord. This opening is called the **foramen magnum**. On either side of the foramen magnum are two irregular bony masses, the **exoccipital bones**. These are separated from each other above and below by a small piece of cartilage. On their posterior end and the side of the foramen magnum these bones bear two oval convex prominences the **occipital condyles** which articulate with the atlas or the first vertebra. Externally each condyle bears an exit hole for vagus nerve. Surrounding the anterior end of the cranium lies a bony ring the **sphenethmoid** or the **girdle bone**. The front part of the ethmoid bone (or **sphenethmoid**) is widened out and divided into two right and left, cavities by a vertical partition. In these cavities are lodged the olfactory sacs. Ethmoid is overlapped by the **frontoparietals** on the dorsal side and **parasphenoid** ventrally. The **frontoparietals** are two membrane bones united along the middle line by the sagittal suture. These are long and flat bones forming most of the roof of the brain-case and overlapping the hinder end of the girdle bone. Each of the frontoparietals is made up of two bones the frontal and the parietal, which are distinct in the early stage of development but fuse afterwards. The parasphenoid also known as the **parabasal** is a large inverted "T" (i.e. "T"-shaped) membrane bone on the ventral side of the cranium; the lateral processes of the bone underlie the auditory capsule.

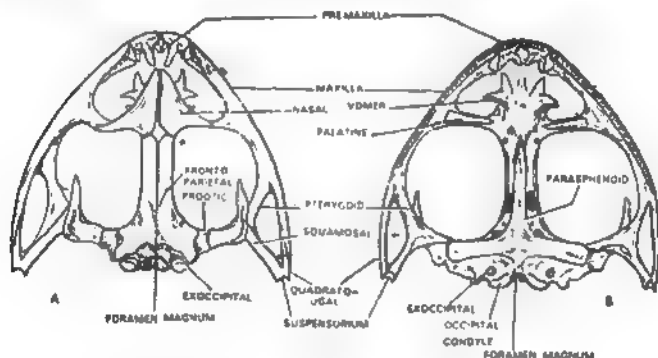


Fig. 5.5. Skull of the frog. A, dorsal and B, ventral views.

Sense capsules are cartilaginous and bony capsules which surround and protect the olfactory, auditory and optic organs. Two of these are fused with the bones by their sides, i.e. with the cranium. (i) The auditory capsules consist of cartilage and are fused with sides of the posterior end of the cranium. The **pro-otic**, a pair of irregular-shaped bones, lie at the sides and in front of the exoccipitals. Each forms a ring-like lateral projection on either side. On the anterior side of the prootics there are apertures serving as exits for the 5th, 6th and 7th cranial nerves. (ii) The olfactory capsules are fused with the anterior end of the cranium. These may also be said to fuse with each other. Membrane bones of the olfactory capsules include the **nasals**, two narrow bones lying on the dorsal side. They are triangular in shape. The bases of the triangular nasals meet in the middle line, they are separated from the fronto-parietals by the sphenethmoid which is visible as a diamond-shaped patch on the dorsal surface. The

vomers are two triradiate bones—having three outer processes. Between the two processes occur the **internal nares**. They lie on the ventral side of the nasal capsule. Each bears on its posterior angle and ventral side a group of pointed teeth, the **vomerine teeth**. (iii) The **optic capsules** remain cartilaginous throughout, and comprise the **sclerotic coat** of the eyes. They are not fused as others.

Upper Jaw. The upper jaw also known as the **maxillary arch** is divided into three parts, (i) **quadrato-jugals**, (ii) **maxilla** and (iii) the **premaxilla**. The **quadrato-jugals** are short bones devoid of teeth forming the posterior part of the arch. It joins the maxilla anteriorly by an oblique suture and towards the posterior end it articulates, with the **pterygoid** and **squamosal**. The **maxilla** is the largest bone furnished with teeth. Its posterior end is joined with the quadratojugal and anteriorly it is joined to the premaxilla. It is provided with teeth throughout its length and dorsally gives off a **frontal process** overlapped by the nasal. The **premaxilla**, also bearing teeth like maxilla, is a small bone joined in the middle with its companion and posteriorly to the maxilla. Both form the apex of the upper jaw. On its dorsal side it gives off backwardly projecting processes which form part of the inner boundary of the nostril.

Suspensorium. The jaws are attached to the cranium by means of an intermediate suspensory apparatus, the **suspensorium**, made up of several separate parts. The **squamosal** is a T-shaped bone on the dorsal side of the skull, the stem of which is closely applied to the angle of the jaw. The posterior limb of T-articulates with the prootics while the anterior end extends obliquely downward in front. The **pterygoid** is a triradiate bone below the squamosal. The inner limb of this bone runs beneath the long stem of the squamosal to connect itself with the angle of the jaw; the outer runs anteriorly joining the maxilla at about its middle while the third joins the outer side of the prootics.

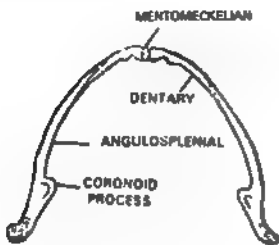


Fig. 5.6. Lower jaw.

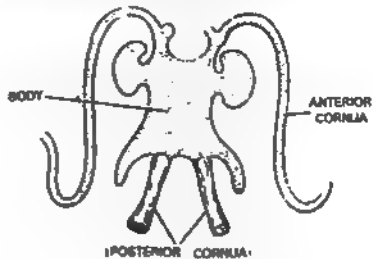


Fig. 5.7. Hyoid apparatus.

The **palatine** is a slender transverse rod-like bone extending from the anterior end of the sphenethmoid and meeting the upper jaw where the pterygoid meets it.

The **quadrate cartilage** is visible in the chondrocranium, but in the fully ossified skull it is concealed between the squamosal (dorsally) and pterygoid (ventrally).

Projecting from the sides of the auditory capsules will be seen the partially ossified hyomandibular cartilage which now forms the **columella auris**.

Lower Jaw. The mandibular arch consists of the Meckel's cartilage partly surrounded by two membrane bones. Meckel's cartilage may be said to be the basis to the lower jaw. The **angulare** or the **angulospheamal** is one of the membrane bones surrounding Meckel's cartilage. This bone lies at proximal end. Near its hinder end it is produced upwards into a prominence, **coronoid process**. The purpose of the coronoid process is to give attachment to the muscles for closing the jaw. The **dentary** is the second bone overlapping Meckel's cartilage. It lies on the outer side of the distal end of the angulare. Here the cartilage runs between these two—the angulare and the dentary. The tip of the lower jaw consists of two short movable bones, the **mentomeckelian**. If these bones are raised the premaxillae are also raised. The

mentomeckelians are formed by the ossification of the distal end of Meckel's cartilages.

Hyoid Apparatus. The remains of the branchial arches of the two sides and the hyoidean arch go to form the hyoid apparatus, which consists of a body and anterior and posterior horns. The body of the hyoid is a flat cartilage, more or less quadrangular in general outline. It lies in the floor of the mouth. All its angles give rise to short processes. Of these the **anterior cornua** are on the anterior margin. These are two long slender rods of cartilage, each of which runs upwards and backwards on either side of the neck and joins the prootic bone behind. The **posterior cornua** are a pair of stout bony processes diverging from the posterior margin of the body of the hyoid. They are also known as the **thyroid processes**.

Vertebral Column These animals have to carry the weight of the body on four legs. This places entirely new set of stresses on the vertebral column, which is largely bony and articulated together because flexibility (needed by the vertebral column of fishes) becoming less important than strength. The new types of strain involve new muscle attachments and the development of special processes and parts of the vertebrae.

In the anurans the entire skeletal and muscular system has become specialized in response to the peculiar mode of swimming and jumping. These movements depend upon extensor thrusts of both hind limbs, acting together. Frogs (and especially toads) also walk on land bringing into play a set of myotatic (proprioceptor) reflexes that depend on the contraction of the muscles against an external resistance. In the primitive vertebrates (fishes) the myotomal muscles produce metachronal waves of contraction imparting flexibility to the vertebral column. In the frog the muscle is attached to the pelvic girdle and acts as a support by which the movement of the hind limbs is transmitted to all the rest of the body.

The vertebral column of the frog consists of nine vertebrae and the tenth is the **urostyle**, a long rod-like bone extending from the ninth vertebra to the apex of the pelvic girdle. A typical vertebra say the third, has typical parts of a vertebrae. The **centrum** is oval in cross section and concave in front and convex posteriorly (**procoelous**). The **neural arch** encloses the **neural canal** and is drawn out into a **neural spine**. At the sides it bears a pair of elongated **transverse processes** which extend almost at right angles to the body. The tips of the transverse processes bear cartilaginous **epiphyses**. The neural arch also bears both the articulating processes the **anterior and posterior pre- and post-zygapophyses**.

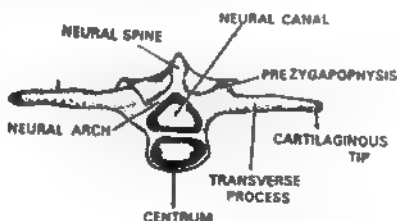


Fig. 5.8. Typical vertebra.

The first vertebra is highly specialized, because it has to support the skull on its anterior face. It is small and is devoid of transverse processes and bears in front a pair of oval concave facets for the articulation with the occipital condyles. The neural arch is well developed and does not bear prezygapophyses. The eighth vertebra is also specialised, being **amphicoelous** (both the surfaces of the centrum are concave). The ninth vertebra is **acoelous**, i.e., no surface of the centrum is concave. Anteriorly the centrum presents a single convexity and posteriorly a pair of convexities for articulation with the urostyle. The transverse processes of the ninth vertebra are very strong and directed obliquely backwards articulating with the ilia of the pelvic girdle.

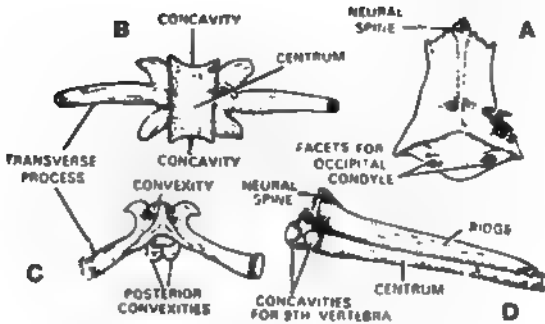


Fig. 5.9. Special vertebrae, A, first, B, eighth, C, ninth vertebrae, D, urostyle.

The **urostyle** is a long bone articulating with the ninth vertebra. On the dorsal side it is elevated into a prominent keel which extends nearly to the posterior end. The anterior face possesses a pair of cavities for articulation with the ninth vertebra. The vertebral canal is small and triangular in outline. There is a pair of small openings through the sides of the urostyle near the anterior end for the exit of the last pair of spinal nerves.

The centra of the vertebrae are joined together by means of pads of hyaline cartilage. Connecting ligaments extend along both the dorsal and ventral surfaces of the centra. The arches and neural spines are joined by ligaments. The spinal nerves make their exit through the intervertebral foramina, between the sides of the neural arches.

Pectoral Girdle The pectoral girdle surrounds the anterior part of the body in the manner of a girdle and protects the inner organs, e.g., heart, lungs and liver, etc. It also gives support to the fore-limbs. It is made of two half rings one on each side of the body. Each half ring bears, in the middle of its hinder surface, a cup, the **glenoid cavity** or **fossa**, with which the first bone of the fore-limb articulates. The portion of the ring above the cavity is the **scapular** portion and that below is the **coracoid** portion. Coracoid portion may be divided into two divisions - anterior and posterior.

Scapular portion has got two parts the **suprascapula** and the **scapula**. The **suprascapula** is flat, distally expanded cartilage. It is calcified (calcium deposited on the cartilage) in order to make it harder. Suprascapula holds the body around the back and covers the first four vertebrae dorsally. Below it is the second part of the scapular portion, the **scapula**. It is an oblong bone constricted in the middle forming the upper half of the glenoid cavity which receives the head of the first bone of the fore-limb.

Of the bones forming the coracoid portion, the coracoid is a stout bone, constricted in the middle and with its inner extremity broadened. The other end forms the other half of the glenoid cavity. This bone connects the sternum with the posterior end of the scapula. There is one slender cartilage, the **procoracoid**, running from the anterior edge of the scapula to the sternum. At the lower end of the scapula is a cartilaginous projection, the **acromion**. The **clavicle** is a slender membrane bone, closely applied to the anterior extremity of the procoracoid. The scapular end of the clavicle is bent forward and is applied to the acromion at the lower end of the scapula. The **epicoracoids** are a pair of two almost calcified cartilages. They are joined with each other in the middle and lie between the ventral ends of the procoracoids and coracoids.

The **sternum** is the portion lying in the mid-ventral line. The following are its parts from before backwards (i) the **episternum** is a circular plate of cartilage lying in front of the omosternum, (ii) the **omosternum** is a slender bony rod lying in front of the clavicles, (iii) the **mesosternum** lies behind the coracoids. It is a rod of cartilage ensheathed in bone; (iv) the **xiphisternum** lies at the hinder end of the sternum. It is broad expanded plate of cartilage.

Fore-limb. The fore-limb consists of one long bone called the humerus, two bones of

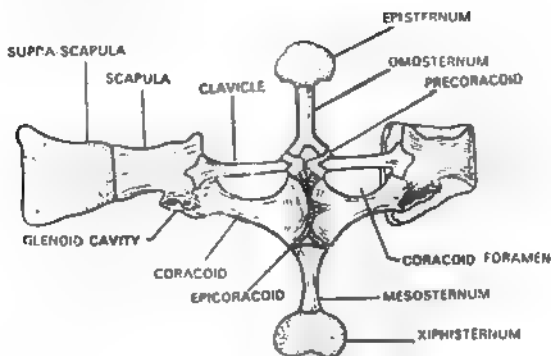


Fig. 5.10. Pectoral girdle.

the arm and several bony pieces and rods forming the wrist and fingers. The **humerus** supports the fore-limb. It has a round ball-like **head** on its proximal end which fits into the glenoid cavity. Its lower end has a rounded prominence in the middle on either side of which is a small projection known as the **condyle**. On the ventral side of the humerus is a large crest, the **deltoid ridge** starting from the head of the humerus almost to the half of its length.

The skeleton of the fore-arm consists of the bone **radio-ulna**. In the dried skeleton of the matured frog the radio-ulna is only one bone but basically this bone is formed by the fusion of two bones the inner one called the **radius** and the outer one the **ulna**. In a young frog these bones are separate, but in old one they are combined. The line of union between the radius and the ulna is very distinct especially at the distal end. The ulnar or the postaxial part projects forwards at its upper end and fits over the rounded end of the humerus at the elbow. This projection is known as the **olecranon process**. The distal end of the radio-ulna is widened and ends in two epiphyses, one for each of the component bone. The wrist or the **carpus** of the frog consists of six bones arranged in two rows of three each. The proximal row is just in contact with the radio-ulna and the distal is the second. Each has got three bones, that opposite to the ulna is known as the **ulnare**, that opposite to the radius is the **radiale** and the middle one the **centrale**.

The hand of frog consists of four very prominent fingers and one rudimentary thumb covered over with skin, as such, is not very prominent like that of the man. There are four prominent **metacarpal** bones succeeded by small bony pieces, the **phalanges**. The phalanges vary in number in different digits. The first digit has got one metacarpal and two phalanges (Fig. 5.4). This corresponds to the fore finger of man. The second one, corresponding to the middle finger, has got one metacarpal and two phalanges. The third corresponding to the ring-finger of man consists of three phalanges and one metacarpal. The fourth one has got three phalanges and one metacarpal bone. This is also known as the postaxial thumb or pollex or the preaxial digit consisting of a metacarpal bone covered over by skin.

Pelvic Girdle The pelvic girdle gives support to the hind-limbs. In construction it is similar to that of pectoral girdle's. It is V-shaped mass of bone the apex of which lies at the posterior end of the skeleton and receives the tip of the urostyle, and the two limbs of the girdle receive the two transverse processes of the sacrum. Each half ring of the girdle is composed of the three bones the **ilium**, the **ischium** and the **pubis**. Almost in the middle of the ring there is a cavity corresponding to the glenoid cavity and known as the **acetabulum**, which receives the thigh bone of the hind-limbs.

The **ilium** forms the upper half of the acetabulum. It is a long bone corresponding to the scapula bone of the anterior girdle. In front, it is attached to the sacrum and to its fellow below. On the dorsal side there is a thin **iliac crest**. The **iliac symphysis** is in the

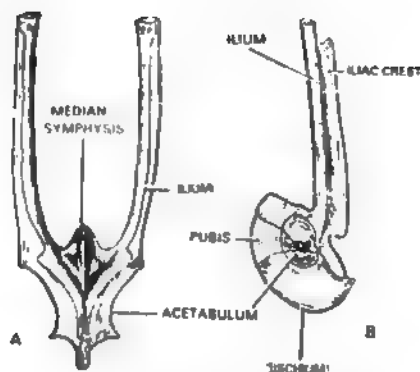


Fig. 5.11. Pelvic girdle. A, dorsal view; B, side view.

median plane at the union of two ilia. The **pubis** is a triangular hyaline cartilage forming about one-sixth of the lower side of the acetabulum. In older frogs it is calcified cartilage. It is on the ventral side of the pelvic girdle and corresponds to the clavicle of the pectoral girdle. The **ischium** is the posterior portion of the pelvic girdle forming the posterior part of the acetabulum. It corresponds to the coracoid of the pectoral girdle. The two ischia are completely fused in the median plane. The elongation of the two ilia, the reduction of the pubis and ischium and fusion of these bones with the ilium forming an almost circular mass is very remarkable in the pelvic girdle. It helps the animal very much in leaping.

Hind-limbs. The skeleton of the hind-limbs of a frog has got almost the same construction and the same general character as that of the skeleton of the fore-limbs. Corresponding to the fore-arm, arm, wrist and hand of the fore-limbs, the hind-limb possesses the thigh, the shank, the ankle and foot respectively.

The **thigh** consists of a long bone the **femur** having a knob (**head**) which fits into the acetabulum and the other end is expanded laterally to form the **trochlea**. The **shank** consists of the bone **fibiofibula** corresponding to the radio-ulna. This bone is longer than the femur. It is formed as a result of fusion of two bones the **tibia** and **fibula**. Line of union is shown by a marked groove throughout the whole length. In case of human beings or rabbits tibia is strong bone and larger than the fibula and are separate but in case of frog they are of equal diameter and strength, and fused with each other. The **ankle** consists of two rows of bones called the **tarsus** (ankle). In this case the rows contain only two bones each (not three) and secondly the bones of the proximal row are much elongated than those of the second. Both bones of the proximal row are long bones united together at both ends but separated in the middle. The one opposite to the tibia is known as the **tibiale** or the **astragalus** (Fig. 5.4). The other on the postaxial side is known as the **calcaneum** or **fibulare**. This one is larger of the two. The distal row of the tarsal bones consists of two very small bones.

The **foot**, corresponding to the hand of frog, consists of five elongated cylindrical metatarsal bones. The first and second digit contains two **phalanges** each, the third and fifth three each and the fourth four. In all there are five digits the first or **hallux** is small and corresponds to the great toe of man. On the preaxial side of the foot there is an additional digit the **prehallux**. The extension of the skeleton of the foot and webbing of the digits helps in the swimming movement of the frog. The length of hind legs of the frog gives a good leverage in jumping.

MUSCULATURE

Trunk Muscles. As the ancestral vertebrates moved out of water to the land and

changed the mode of locomotion the muscular system also became modified. Urodeles retain the old method of locomotion and hence their dorsal musculature is well developed, but in anurans the dorsal portions of the myotomes (the epaxial musculature) no longer have to produce the locomotory effect by lateral flexion; they become reduced and bend the body dorsally, and serve to brace up the vertebral column on the sacrum. Short muscles run between the vertebrae, and dorsal to these there is a continuous sheet of longitudinally arranged fibres, the *longissimus dorsal muscle*, running from head to the sacral vertebra and urostyle. This continuous muscle band is derived from segmental muscles as is evidenced by a number of tendinous intersections which cross it. At the posterior end of the body the *coccygeo-sacralis* and *coccygeo-iliacus* muscles brace the urostyle on the pelvic girdle.

There are a series of muscles that bind pectoral girdle to the axial skeleton. From the suprascapula *rhomboid* and *levator scapulae* muscle run to the vertebrae and skull. The *occularis* muscle, derived from the lateral plate musculature, runs from the skull to the suprascapula. It is innervated by the vagus.

The hypaxial musculature is more developed than in fishes, and is differentiated into several parts to support the viscera which needs better support on the land than in water. These muscles are differentiated into layers whose fibres run in different directions. Three sets of these fibres can be recognized in the adult frog. In the mid-ventral region are the longitudinally arranged fibres of the *rectus abdominis*, extending between the sternum and the pubis. Transverse fibrous tendinous inscriptions interrupt these fibres at intervals, giving an appearance of segmentation to them. A tendon having no muscle fibre, the *linea alba*, extends in the mid-ventral line. The *obliquus externus* and *transversus abdominis* are the thin sheets of muscle fibres supporting the sides. In the anterior region the hypaxial muscles have become restricted to the throat, where they form the *hyoid musculature*, which are meant to raise and lower the floor of the mouth during breathing. The *submaxillary* muscle runs transversely between the rami of the jaw.

Limb Muscles. The muscles of the limbs have presumably been derived from the radial muscles that moved the fins. The muscles of the modern amphibians arise independently in the mesenchyme of the limb. There is no evidence that the limb musculature has been derived from the myotomes. The segmental origin, however, is established by the fact that the limb muscles are innervated by branches of the spinal nerves of several segments. The muscles of the fore-limb of the frog are innervated by spinal nerves of two segments and hind-limb by four segments.

In the fore-limb there is a sheet of fibres running transversely to the main axis of the body and attached to the sternum and hypaxial muscles at one end and to the humerus at the other. Within this sheet occur the *deltoides*, *pectoralis*, *coracoidialis* and *coracobrachialis* muscles. This group is continued in the limb also. Roughly speaking there is a set of muscles in each segment that serves to flex it on the next. Thus the *brachioradialis* flexes the elbow-joint and in the forearm the *flexor carpiradialis* and *flexor carpi ulnaris* flex the wrist. The *flexor digitorum longus* muscle arises from the medial epicondyle of the humerus and is inserted to the carpus and terminal phalanges by tendons. The *flexor digitorum brevis* muscles arise from this tendon for insertion on the digits. Two muscles, the *latissimus dorsi* and *dorsalis scapulae*, run from the middle of the back to the humerus and serve to abduct and draw back the whole limb. The *triceps* (anconeus) are extensors of the elbow and in fore-arms are the *extensor carpi ulnaris* and *radialis* and extensors for the fingers. According to this plan protractor (flexor) muscles lie mainly anterior to retractors (extensors) corresponding to the ancient movement by which the limb was drawn first forward and back as a swimming wave passed down the body.

In the hind limb muscles of the same two general types occur. These are the anterior muscles which draw the limb forward and flex and abduct its joints, and posterior ones which draw it back and extend and abduct. The anterior muscles of the thigh include the *pectineus* and *adductors* running from the pelvic girdle to the femur. They move the whole limb inwards (adduction). The *sartorius*, *biceps*, *semi-membranosus*, and *semitendinosus* are two-joint muscles mainly producing flexion at the knee as well as at the hip. The posterior muscles include the *gluteus* and *tensor fascia lata* extending

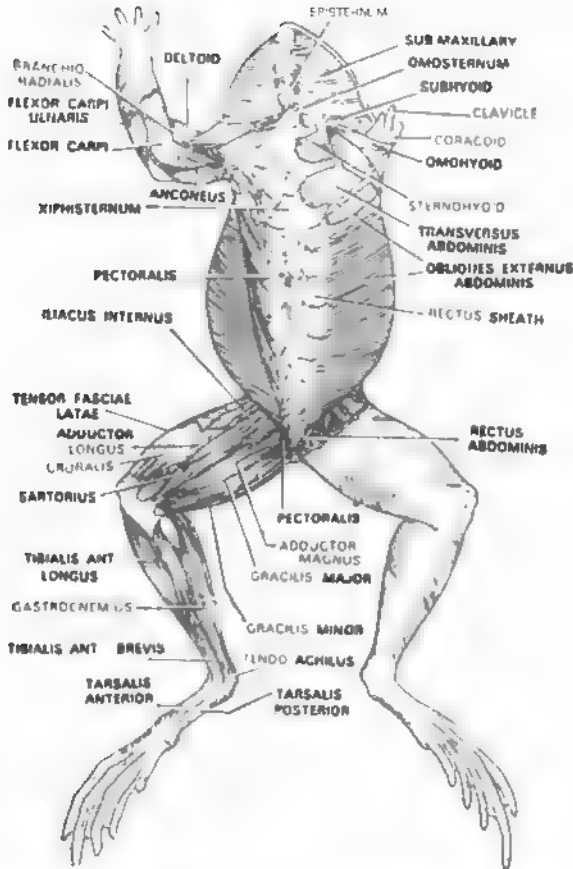


Fig. 5.12. Musculature of *Rana temporaria* exposed from ventral side (after Gaupp).

from girdle to femur across the thigh joint. The large **cruralis** (including the **rectus femoris** and **triceps femoris**) runs from girdle and femur to tibia. This is the main extensor of the knee. It is helped by **gracilis** and **semimembranosus**. Obviously the extension of the knee is an important part of the jumping movement of frog. The muscles that flex the ankle-joint include the **tibialis anterior** and **peroneus** extending from the femur to the tarsus. The **gastrocnemius** (**plantaris longus**) runs from the femur and is attached to the tarsus through the tendon called **tendon of Achilles**. It is at the back of the tibiofibula and extends the ankle in swimming or jumping. Another muscle the **tibialis posterior** runs from tibia to the tarsus. There are long and short flexors that move the toes, in fact there is an elaborate system of small muscles for bending and stretching the toes and abducting them away from each other, so as to expand the circle and help in the swimming movement.

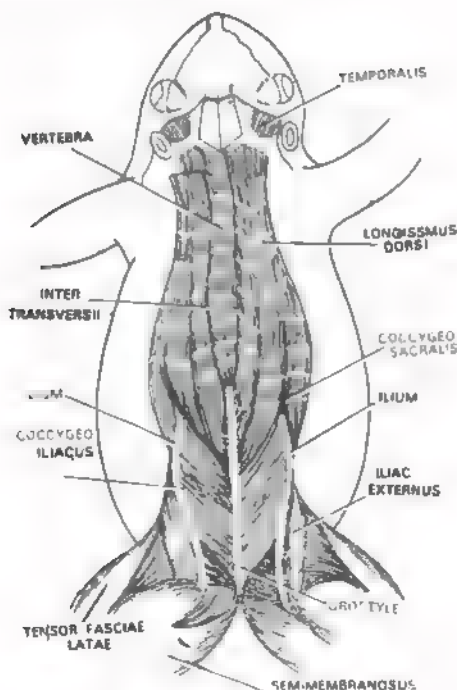


Fig. 5.13. Muscles of the back of frog (after Gaupp).

BODY CAVITY

The body cavity of the frog is relatively large and is without partition as in higher vertebrates. All the internal organs, **viscera** are lodged in the body cavity, the **splanchnocoel**, derived from the embryonic coelom. The viscera is suspended in the body cavity and is covered by the coelomic epithelium, the **peritoneum**. In some cases the coelomic epithelium is pulled out into double sheets between which connective tissue is laid down to form **mesenteries**. Various organs in the body cavity are slung from the dorsal wall of the body cavity or connected with one another by mesenteries. On the anterior side of the main body cavity a small **pericardial cavity** is cut off. This is enclosed by an extension of the peritoneum called **pericardium** and lodges the heart. In embryo the coelom is very spacious but it becomes considerably reduced in the adult as various organs enlarge. The coelom is filled with **coelomic fluid** secreted by the epithelium. This fluid acts as a lubricant and enables the viscera to slip easily over one another.

DIGESTIVE SYSTEM

The digestive system (includes the alimentary canal, where the process of digestion and absorption take place, and the **digestive glands**, whose secretions bring about digestion. The alimentary canal includes the **buccal cavity**, **pharynx**, **oesophagus**, **stomach**, **intestine** and **rectum**).

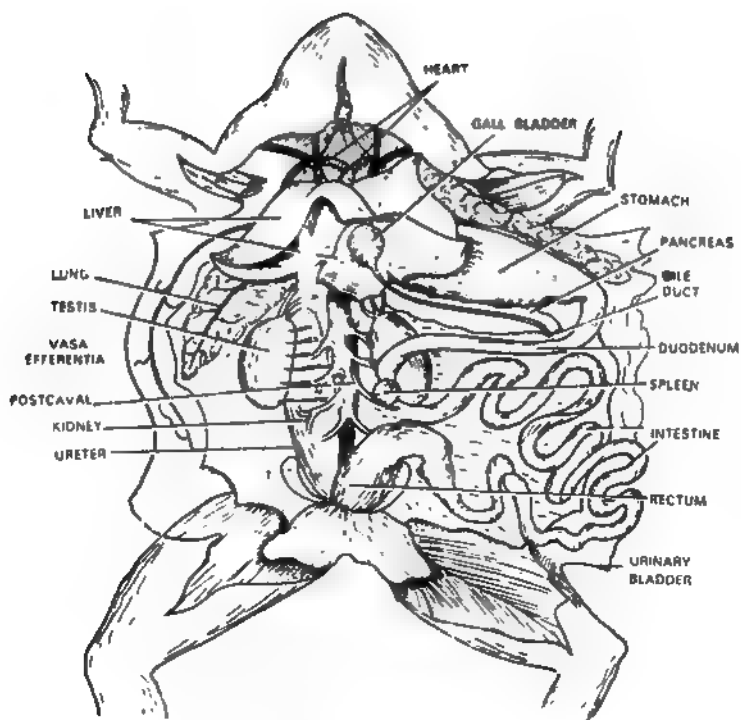


Fig. 5.14, Dissection of the frog to show the internal viscera

Buccal Cavity. Within the upper and lower jaws is the broad buccal cavity. The buccal cavity is derived from the stomodaeum and consequently is lined by ectoderm and the mouth aperture opens directly into it. The mouth is terminal and wide. This narrows behind as the pharynx which leads into the gullet or oesophagus. The

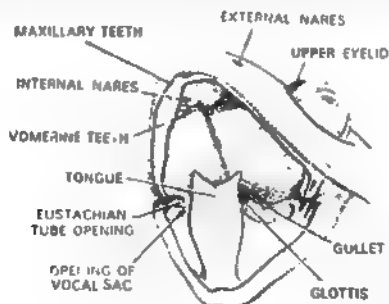


Fig. 5.15, Mouth cavity opened to show internal structure

entrance to the lung or the **glottis** is also situated in the pharynx. It is a median ventral slit-like opening behind the tongue. It is opened for breathing, the closes while food is being swallowed. A protrusible tongue is present in the floor of the bucco-pharyngeal cavity. The attachment of the tongue is unusual. Ordinarily the tongue is attached at the back of the buccal cavity and projects forwards, but in the frog the point of attachment of the tongue is anterior, immediately within the margin of the lower jaw (Fig. 5.15). This helps in feeding. The tongue can be "whipped" out with a remarkable rapidity and being attached in front it can not only cover greater distance in front but is withdrawn quickly. The protrusion is brought about by the change of pressure in the large sublingual lymph sac. According to Hartog the contraction of the mylopharyngeal muscles expels the lymph from the subhyoid space into the tongue and this effects the protrusion of this organ.

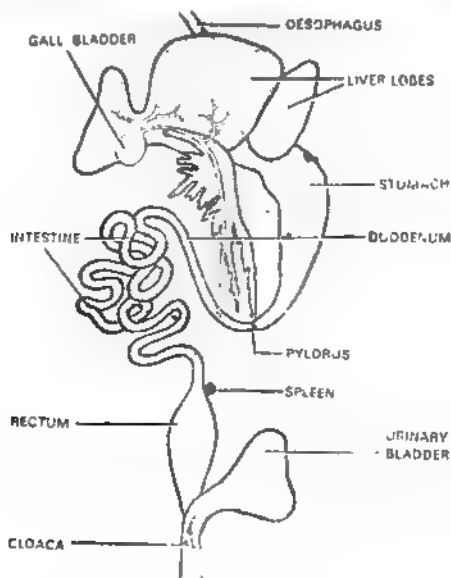


Fig. 5.16. Alimentary canal of the frog.

The buccal cavity is wide from side to side and in its floor beneath the tongue, lies the body of the hyoid. The hyoid brings about the raising and lowering of the floor of the lower jaw thereby decreasing or increasing the internal capacity of the bucco-pharyngeal cavity. This arrangement is used in respiration. At the anterior end of the buccal cavity the two **internal nares** are present. They communicate with the exterior through the olfactory organ and the external nares. The epithelium of the buccal cavity is richly supplied with mucous glands and is also profusely ciliated. The **pharynx** is imperfectly delimited from the buccal cavity. Into the pharynx open the Eustachian tubes by two wide laterally placed apertures. These lead into the tympanic cavity of the middle ear.

Teeth. The upper jaw of the frog bears teeth, the lower jaw is without them. The vomers in the roof of the upper jaw also bear teeth. The teeth are small in size and uniform in structure. The teeth of the jaw rest against the dental processes of the maxillary and premaxillary bones and are attached by cement substance. Most of the teeth are embedded in the mucous membrane, only a little portion of each projects

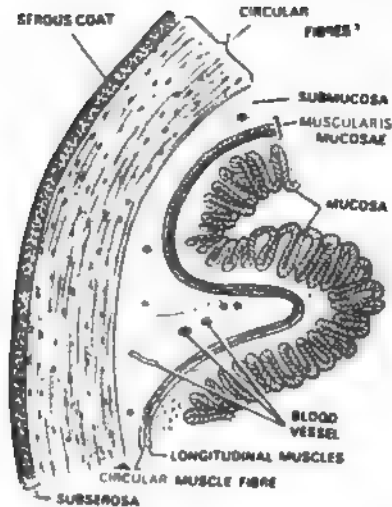


Fig. 5.17. A portion of the cross-section of stomach of the frog.

out. Each tooth is more or less cylindrical in form tapering towards the upper end. Each tooth is somewhat incurved. The basal portion of the tooth forms the root by which it is attached to the jaw. The free end or crown is separated from the root by a transverse furrow. The central pulp cavity is filled with a very vascular tissue or pulp. The pulp also contains **odontoblast cells**, which produce new material for the growth of the tooth. The greater part of the crown is composed of **dentine** traversed by numerous fine branching canals, leading from the pulp. The upper half of the crown is coated with a very hard resistant layer, the **enamel**. The root of the tooth is made up of material that resembles bone in nature and composition. The teeth are not masticatory in function, but are used to hold the prey. The old and worn out teeth are being continuously renewed throughout life, ceasing only in the old individual. New teeth are produced below the old ones which are cast out.

The pharynx leads into the **oesophagus** a short tube whose inner lining is folded longitudinally to allow for expansion during the passage of food through it to the stomach. The **stomach** is a thick-walled slightly dilated portion of the alimentary canal. The stomach terminates at the **pyloric constriction**, but there is no bending of tube or its division into regions. The stomach is larger at the anterior or **cardiac end** and tapering towards posterior or **pyloric end**. The wall of the stomach is thick and is made up of six layers: (i) the **mucosa** or inner lining with many glands, (ii) the **submucosa**, a network of connective tissue containing blood and lymph vessels and nerves, (iii) the **muscularis mucosae** with both circular and longitudinal bundles of smooth muscle fibres, (iv) the layer of circular fibres which becomes thicker towards the pylorus, (v) **subserosa** or outer connective tissue layer, and (vi) the **serosa** which is the peritoneum. The subserosa has been frequently described as a layer of longitudinal muscles which it apparently looks like. The mucosa of the stomach is a thick layer composed of glands embedded in a supporting matrix of connective tissue. These glands have been formed by invaginations of the epithelium lining the inner surface of the stomach. They are elongated tubular structures set very closely together, and frequently, more or less, branched. The glands differ in structure at the two ends of the stomach. They are very long with deep set mouth lined with elongated cells in the cardiac region. In the pyloric end the glands are less deep and smaller (Fig. 5.18 B). Histologically the oesophagus

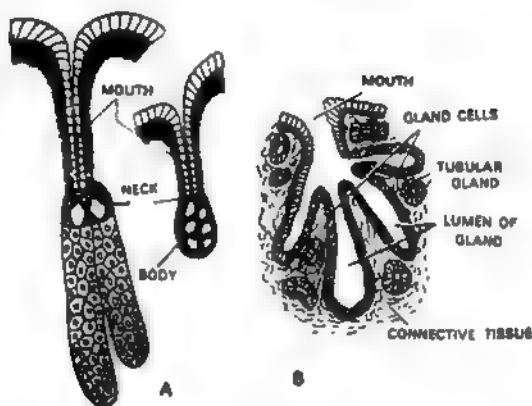


Fig. 5.18. Different types of gastric glands of the frog's stomach. A, from cardiac end; B, from pyloric end; C, ordinary gland from the middle.

resembles the stomach in a general way. There is an external layer of longitudinal muscle fibres, but both are relatively thin. A muscularis mucosae is lacking except near the stomach. The mucosa is well developed.

The stomach leads into the intestine, the first part of which is called the duodenum although it is not clearly demarcated from the rest. The duodenum is the portion into which opens the common hepatopancreatic duct. The remaining portion is called the small intestine or ileum, which after coiling about in an irregular manner widens into the large intestine. The intestine is the longest part of the alimentary canal. This absorbs the digested food. The absorptive space is further increased by the folding of the inner lining of the intestine. The intestine is suspended by a fold of mesentery to the mid-dorsal portion of the body cavity.

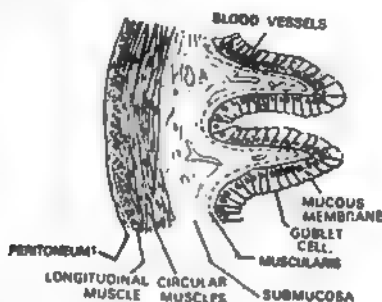


Fig. 5.19. Transverse section of ileum of the frog.

The intestine is covered by a thin coat of peritoneum within which lies the musculature consisting of smooth muscle-fibres. The musculature is differentiated into two layers, an outer well-marked layer of longitudinal muscle fibres, and an inner thicker layer of circular muscle fibres. Within the musculature lies the submucosa, connective tissue layer containing numerous blood vessels. The submucosa is followed by the mucosa. The connective tissue portion of the mucosa is more dense and

contains more cellular elements. Between the mucosa and submucosa are large irregular lymph spaces which frequently extend into the folds. The muscularis mucosae is absent although some investigators have affirmed its presence.¹ If this layer is present then it may be represented only by a few scattered cells. The epithelium of mucosa consists of cylindrical cells of two types, larger goblet or breaker cells and ordinary absorptive cells. The goblet cells may contain oval vacuoles. The inner end of the cells is filled with a transparent, more or less, granular substance, which probably produces mucous. The nucleus is situated near the base of the cell. The absorbing cells are narrow, with oval nuclei near the base. The mucosa of the small intestine is thrown into numerous folds, but there are no true villi, nor definite glands nor crypts such as occur in the higher vertebrates.

The small intestine leads into the large intestine or rectum, the transition from one to the other being rather abrupt. The rectum passes straight back and opens into the cloaca. The large intestine is composed of the same layers as the small. The inner surface is thrown into folds, which at the proximal end form an irregular net-work, but in the rectum they become longitudinal. The epithelium of the mucosa consists of cylindrical cells among which numerous goblet cells are to be found.

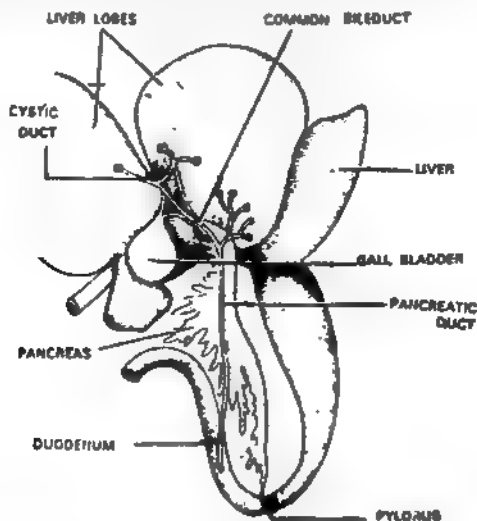


Fig. 5.28. Liver lobes, pancreas and its ducts.

Digestive Glands. There are two important digestive glands, viz., the pancreas and liver. The pancreas is an elongated gland lying in the mesentery between the stomach and the duodenum. It is traversed by the common bile duct into which ducts from the pancreas also open. Of these there is a principal pancreatic duct and several smaller ducts from the portions of the gland near the liver. The pancreas is a much-branched tubular gland, the terminal branches of the glands being often curved and twisted in an irregular manner. The tubules are coated externally with basement membrane and held together by connective tissue in which lie the blood vessels and nerves. In a transverse section larger number of circular, oval or variously-shaped surfaces are seen packed together. These are the tubules of the glands in sections. The secretory cells of the tubules contain numerous zymogen granules, which occur in abundance when the

1. No sections cut and examined by the author shows any indication of the presence of muscularis.

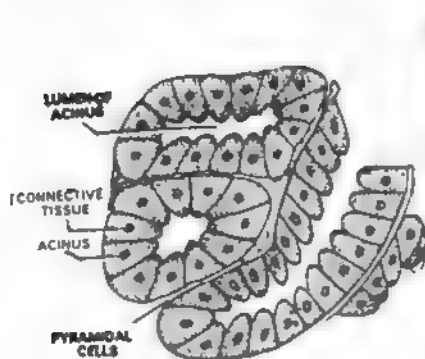


Fig. 5.21. Transverse section of pancreas.

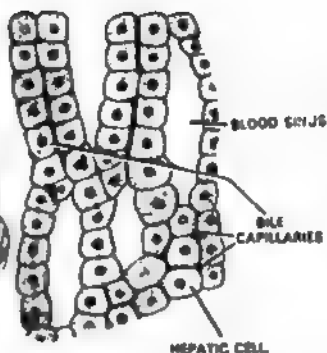


Fig. 5.22. Cross-section of liver

frog is hungry and disappear when the animal is fed. The fluid secreted by the pancreas is alkaline (due to the presence of sodium carbonate) and contains three enzymes : **steapsin or lipase, amylase and trypsin.**

Liver. The liver is a large gland whose secretion, the **bile**, is conveyed to the intestine through the bile duct, along with the pancreatic secretion. The liver is made up of two lobes of which the left is again subdivided into two. The entire gland is of dark-red colour and is supported by a fold of mesentery. Between the main lobes lies the spherical **gall bladder** from which arises the bile duct, which also receives the supplementary ducts from the main lobes of the liver. On its way to the duodenum the bile duct passes through the substance of the pancreas and receives its ducts. The secretory cells of the liver are cubical or polyhedral (Fig. 5.22) in form with large nuclei. They are arranged in parallel longitudinal rows appearing like columns or cords. The cytoplasm of the liver cells contains protein granules, small drops of fat, lumps of glycogen and often pigment. In between the liver cells occur ultimate branches of the hepatic ducts or **bile capillaries**. Basically each liver is a much-branched tubular gland and a section through it should look like that of the pancreas. But this is not so because the bile capillaries branch and anastomose in an irregular manner so much so that the original tubular structure of the organs is obscured. The liver receives arterial blood through the **hepatic artery** and also from the portal system, which includes the anterior abdominal vein from the ventral body wall, and the hepatic portal vein from the stomach, intestine, pancreas and spleen. All the material absorbed by the blood from the digestive organs passes through the liver before entering the general circulation. The liver is also supplied with lymph vessels which form perivascular lymph spaces around the capillaries. The liver of the frog generally contains a considerable amount of pigment. Two forms of pigment have been reported, the black or dark-brown and golden. The granules of the liver cells are of secretory nature, as such they increase in number after meal.

A dark-red spherical body, the **spleen**, is attached to the mesentery between the ileum and rectum. It is found in intimate association with the alimentary tract but has nothing to do with digestion. It is a well-developed lymphoid structure which not only gives rise to new blood corpuscles but disposes of the old ones.

NUTRITION

Food. Some animals feed exclusively upon vegetable material and are called **herbivorous**; others feed on the bodies or flesh of other animals and are **carnivorous**. Some eat both and are **omnivorous**. Whatever form the food stuffs may take they must contain the essential material for the building up of new protoplasm and for the supply

of energy for vital processes. Needs of animals are fully supplied by the following types of chemical substances.

Carbohydrates
Proteins

Fats
(Mineral Salts)
(Inorganic)

Water
Vitamins

Among the familiar carbohydrates are sugars, and starches and cellulose; proteins comprise a large part of solids of the protoplasm of plant cell, the flesh of vertebrates, cheese, yolk of eggs; fats occur in animal and vegetable oils and most animal tissues. Mineral salts, e.g. chlorides sulphates of sodium and potassium, carbonate and phosphates of calcium, potassium, magnesium, and sodium and various salts of iron are used in many metabolic processes. Vitamins are complex organic substances normally taken in with the foods and are essential to the maintenance of health and for growth.

Ingestion. The frog feeds chiefly on earthworms, spiders, etc., which it swallows whole. It is carnivorous. Its method of catching its prey is rather remarkable, because it can catch insects on wing. When feeding it squats in a suitable place frequented by insects and when one flies near, it opens its mouth and flicks out its tongue and strikes the insect with it. The tongue is covered with a viscid, sticky secretion, so that the insect adheres to it and, by a return flash, is brought into the back of the pharynx. From this place it is pushed by the pharyngeal contraction into the oesophagus. The teeth

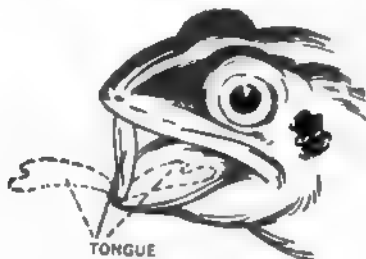


Fig. 5.23 Action of the tongue while catching food

covering the upper jaws are used to seize and hold the food during swallowing. The aid of the prominences of the eyeballs is also taken in pushing the food inwards. The movement of the tongue is amazingly rapid and its position of attachment and muscular character enable it to be projected to some distance from the mouth. If any small fragments are left in the buccal cavity they become entangled in mucous secreted by cells in the epithelium and are carried by ciliary currents to the oesophagus.

Digestion. With the exception of the mineral salts and some of the carbohydrates most of the solid food is insoluble and incapable of mixing with water; it forms a colloidal solution and as such is incapable of passing through the lining membrane of the alimentary canal. The food must, therefore, be rendered soluble and diffusible before it can be of use to the organism, i.e. it must be transformed from colloid to the crystalloid condition and this process is called digestion. In all cases digestion consists of a process of hydrolysis during which the molecular size of the substances is progressively reduced until a true solution is possible. These changes are brought about by the familiar organic catalysts known as enzymes. These complex organic substances produced by the lining cells induce with ease and rapidity chemical reactions which would be difficult and lengthy. Under ordinary laboratory conditions each particular enzyme acts only upon a particular substance or group of substance (called substrate) and at the end of the reaction it itself remains unaltered. Enzymes can be rendered inactive or killed by heat and other means. They act best at a

particular temperature called the optimum temperature and require that the medium in which they work shall have a certain alkalinity or acidity.

Enzymes are classified in accordance with the type of substance they act. Thus carbohydrates are digested by diastatic enzymes (carboxylases) proteins by proteolytic (proteases) and fats by lipolytic enzymes (lipases).

In those animals that chew the food as ourselves, the digestion begins in the buccal cavity. During mastication the food is mixed with saliva which contains a diastatic enzyme **ptyalin**. This acts on starches changing them into sugars. Saliva is slightly alkaline but ptyalin acts best in a neutral or very slightly acid medium. The extent to which digestion occurs in the buccal cavity depends upon the length of time it is retained there and the thoroughness of the mastication.

In the stomach the food is subjected to the action of the gastric juice secreted by the gastric glands. This contains 90% water and an enzyme **pepsin** and free hydrochloric acid. Latest workers point out to the presence of another enzyme called **rennin** that coagulates milk in man or rabbit. **Rennin** is not present in the frog. **Pepsin** is proteolytic enzyme that changes proteins into **peptones**. In the stomach there is copious addition of fluid to the food and proteins are converted into peptones and the tissue surrounding fat is dissolved away, fat being liberated as free globules.

The opening of the stomach into the duodenum is guarded by sphincter muscles. The food is thus retained for some time in the stomach (in man for 2 to 3 hours). During this period the walls of the stomach contract and relax thus churning the food thoroughly and mixing it with gastric juice fully. Here it takes the form of a thick creamy acid-fluid called **chyme**.

While the chyme is being formed in the stomach the duodenum secretes a hormone **secretin**, which induces the pancreas to produce its juice and the gall-bladder to release bile. Under these conditions the pyloric sphincter relaxes and the chyme passes down to the duodenum. Here the food meets bile, the pancreatic juice and the **succus entericus** from the wall of the intestine.

Bile is a greenish alkaline watery fluid which contains no digestive enzymes so that it takes no active part in digestion. It is alkaline in nature. It reduces the acidity of chyme and prepares the fluid for the activity of pancreatic juice which can act only in the alkaline medium. The bile pigments (bilirubin and biliverdin) are excretory products as they are produced from the breakdown of haemoglobin of the defunct red blood ~~corpuscles~~.

The pancreatic fluid is a watery alkaline fluid, very rich in enzymes. It contains **trypsin** (proteolytic), **amylase** (diastatic) and **steapsin** (lipolytic). Trypsin, as it is released, is inactive unless mixed with intestinal secretion, **succus entericus** which is produced by the glands of the duodenum and small intestine. It is an alkaline watery fluid containing mucin and many enzymes that complete the digestion.

Thus as the food passes down the duodenum and meets all the above enzymes the proteins are all reduced to amino-acids, the carbohydrates to glucose and other similar sugars and fats to glycerol and fatty acids.

Absorption and Assimilation. Whilst within the alimentary canal, the food although within the confines of the body, is not part of it, for physiologically it is still out of it. In order to be useful to the body it must be absorbed into the blood stream. Practically no absorption of digested food takes place in the buccal cavity, oesophagus or stomach. The absorptive area of the alimentary canal lies within the small intestine. This area is enormously increased by the development of folds called villi (singular villus). These folds or villi have rich blood supply. The digested fats, proteins and carbohydrates diffuse through the walls of the intestine and reach the blood supply and thus enter into direct circulation. As the food passes downwards the excess of water contained in the food residuum is extracted by the walls of the large intestine so that by the time the residue reaches the rectum it is in the form of semi-solid called **faeces**. They are ejected or extruded at intervals through the anus into the cloacal chamber whence to the exterior.

The animals utilise carbohydrates and fats as sources of energy and the proteins are used for building up protoplasm.

CIRCULATORY SYSTEM

The circulatory system of the amphibians is constructed on a plan different from that of the fish. Due to the appearance of the lungs the single circuit heart of the fish undergoes special modifications. In fishes the blood is pumped to the gills and the aerated blood goes to the different parts of the body and returns to the heart after giving off oxygen. In the terrestrial animals the blood flows in two circuits. Blood goes from the heart to the lungs and after oxygenation returns to the heart to be pumped back to different parts of the body. Thus the heart has two separate auricles and there is a mechanism in the ventricle and the truncus arteriosus to avoid mixing of oxygenated and deoxygenated blood.

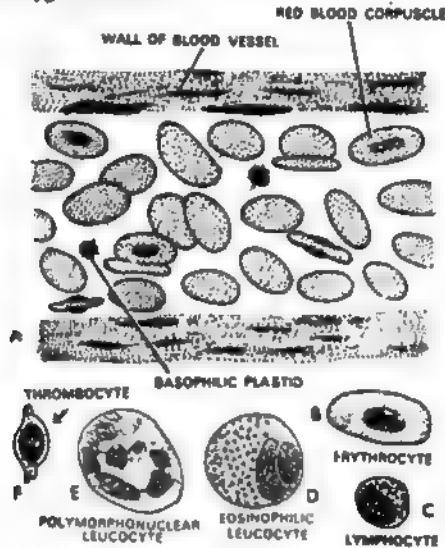


Fig. 5.24. Blood of the frog.

The blood of the frog presents the general structure. The erythrocytes are elliptical in outline and have an oval nucleus in the centre. Seen on edge they appear flattened and slightly bulging in the centre, the place of the nucleus. The cytoplasm of the cell contains haemoglobin. The white corpuscles (leucocytes) vary both in size and form. The cytoplasm of the leucocytes is nearly colourless, but is often granular. The form of nucleus varies being usually spherical in smaller leucocytes. They have independent power of locomotion and are amoeboid. They may pass out of the delicate walls of the capillaries. Both the red and white corpuscles float in liquid plasma.

Heart. The heart is situated in the anterior part of the body cavity, ventral to the liver. It lies within a sac, the **pericardium**, whose cavity is completely cut off from the coelom, although originally continuous with it in early development. The pericardium consists of two layers, the **parietal** forming the outer wall of the sac, and the **visceral** which closely invests the heart.

The heart consists of: (1) The conical **ventricle**, with its apex pointing backwards; this part has very thick muscular walls and appears paler than the rest. (2) The **auricles** are two and lie immediately in front of the ventricle. The auricles are thin-walled and are separated from each other internally by a septum. Externally this separation is not well marked, there is only a faint indication. From the ventricle, however, they are

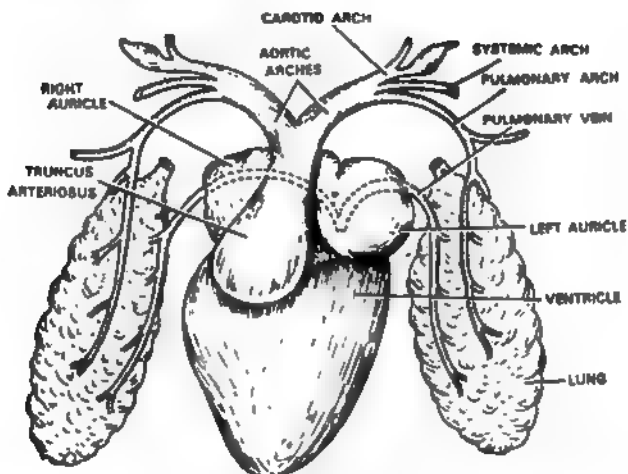


Fig. 5.25. Ventral view of the heart of the frog.

clearly separated by a coronary sulcus. (3) The truncus arteriosus¹ (Fig. 5.25), lies in front of the right side of the ventricle. It is roughly divisible into two parts : (a) a thickened muscular bulb-like conus arteriosus extending the truncus across the right auricle; and (b) the anterior thin-walled narrow tube, the truncus proper, bifurcating

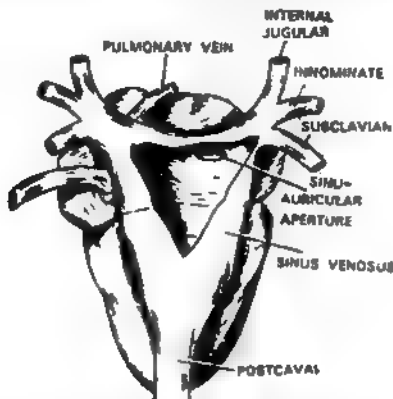


Fig. 5.26. Dorsal view of the heart of frog with a portion of the sinus venosus removed to show its opening into the auricle.

¹ Huxley (1872) called it "bulbus". Ecker (1889) called it "truncus arteriosus". Gegenbaur (1891) used "conus arteriosus" to denote the ventral aorta in elasmobranch and ganoids. Gaupp (1899) in *Rana emporaria* and Holmes in *R. pipiens* used the terms "bulbus cordis" and "truncus arteriosus" for two parts of the vessel. Miss Oliver (1909) called the entire vessel as "truncus arteriosus" and divided its interior into a proximal pylangium and distal synangium. This nomenclature has been used here to avoid confusion because of long usage, although it is preferable to call the proximal part "conus" and the distal part prior to bifurcation as "truncus arteriosus" because of its bulbus and tubular nature.

into two (4) The **sinus venosus** (Fig. 5.26) is the triangular sac situated on the dorsal side of the heart. At the two anterior ends of the sinus enter the two **precavals** and at the posterior apex enters the large **postcaval vein**. Each precaval has a pair of valves at its opening. In front of the anterior margin of the sinus is the pulmonary vein which empties into the left auricle. Careful examination shows that the pulmonary veins lead into a small chamber, the pulmonary recess, which open into the left auricle by a funnel-shaped opening.

The internal structure of the heart reveals a beautiful mechanism for propelling the blood only in one direction and distributing the oxygenated and deoxygenated blood properly. On removing the ventral walls of all the structures the internal structure becomes apparent. The **interauricular septum** projects to some extent in the ventricular lumen and is so situated that the right auricle is much larger than the left. In the right auricle close to the septum is the large **sinuauricular aperture** through which blood enters from the sinus venosus. It is a transverse oval opening guarded by valvular lips (Fig. 5.27) on the anterior and posterior sides. These valves allow the blood to flow in from the sinus and prevent the back flow.

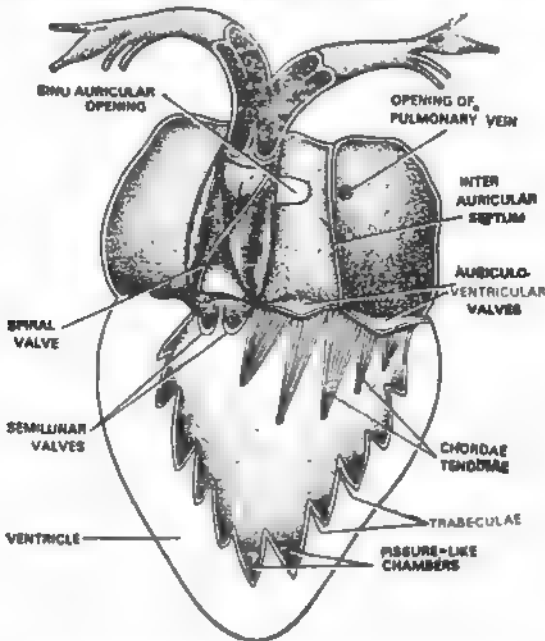


Fig. 5.27. Internal structure of the heart of frog (semi-diagrammatic)

Slightly anterior to the sinu-auricular aperture, in the left auricle, just near the septum, there is a small **opening of the pulmonary vein**. This opening has no valve. But the vein perforates the wall obliquely, hence the pressure caused by the contraction of the auricles serves to close the opening.

Both auricles open into the ventricle by a large opening, the **auriculo-ventricular aperture**, which is divided by the inter-auricular septum. This opening is guarded by 14 valves, two large ones on the dorsal and ventral edges, and a small valve at either end. Small fibres, **chordae tendinae**, arise from the ventricular wall to be inserted into the free edges of the valves to prevent them from being pushed back into the auricles when

the ventricle contracts, and thus keep the blood flowing from the ventricle into the auricles.

In the heart of man or rabbit the ventricle is divided into two chambers thus preventing the deoxygenated blood from mixing with the oxygenated. In case of frog the ventricle is not divided into two. However, in addition to the central cavity the ventricle possesses at its base a number of fissure-like chambers in the thick muscular walls. These chambers are separated from each other by muscular partitions or trabeculae that extend outwardly nearly to the periphery of the ventricle. They receive the blood coming from the two auricles and prevent the mixing of the two samples.

The opening from the ventricle into the truncus arteriosus is guarded by three (four according to Sharma, 1957) semilunar valves. They are in the form of pockets, open anteriorly, whose walls may be pressed down when the blood is passing from ventricle to the truncus, but if the blood tends to pass back the pockets are filled with blood and thus block the passage, the blood now cannot come down again. In the truncus there are three more pocket-shaped semilunar valves placed anteriorly. This set of valves divides the truncus into two parts. (1) the proximal and longer is the conus arteriosus or pylangium, (2) the distal is shorter known as the truncus arteriosus or synangium.

Further the cavity of the pylangium is incompletely divided into two by a membranous fold the spiral valve, that arises in the right ventral side. This traverses the chamber obliquely. It is attached throughout by its dorsal edge and to one of the semilunar valves in front. The ventral edge of this fold hangs free in the cavity of the pylangium incompletely dividing it into a chamber beginning on the ventral side and curving round to right, the *cavum aorticum*, and another beginning on the dorsal side and curving round to the left, the *cavum pulmocutaneum*. Anterior to the spiral valve is an aperture leading to the *pulmocutaneous* arteries. A pair of valves (the dorsal and ventral *pulmocutaneous* valves) guard this opening (Sharma, 1957). It is here that the truncus divides into right and left halves. Soon after the bifurcation are the apertures leading to the systemic trunks, and more anterior still those of the carotid arteries. Sharma (1957) describes a common opening of the systemo-carotid arches in *Rana tigrina*, which is guarded by a pair of systemo-carotid valves, one dorsal and one ventral.

Working of the Heart. The blood from the general body tissues, returning in veins passes into the right auricle when it expands. Simultaneous with this, the blood from the lungs passes into the heart through the pulmonary. Thus, when the auricles are expanded the left auricle contains blood from the lungs and the right auricle contains blood from the body tissues. As the auricles contract the ventricle enlarges and the blood from the two auricles passes into the ventricle. The blood from the left auricle comes to occupy the left side of the ventricle. Next the ventricle contracts and the blood is forced out. As already mentioned, the opening between the auricles and the ventricle is provided with valves which will not allow the blood to pass backward again into the auricles, the blood is forced forward into the conus which itself has a contractile wall.

What happens to the blood as it leaves the ventricle was elucidated by Brücke about one hundred years ago. This view put forward that with the contraction of the ventricle the deoxygenated blood of the right side of the ventricle first passes to the conus. This blood passes into the *pulmocutaneous* arteries, thus, going to the lungs through the pulmonary arteries, and the skin through the cutaneous arteries for oxygenation. As the ventricular contraction proceeds the spiral valve changes its position, so that the blood from the middle of the ventricle is sent mainly up the right side of the spiral valve. This blood goes to the systemic vessels. It does not go to the carotid vessels, for at the bases of the carotid arteries are the structures known as the *carotid labyrinths*, which consist of a network of blood capillaries, and which are assumed to have the function of increasing the resistance to blood flow in the carotid or head circulation. With the ultimate contraction of the ventricle the pressure rises and the blood flows into the head. This is the blood from the left side of the ventricle, i.e., the blood from the left auricle which is returned from the lungs. Although the ventricle is undivided yet a perfect double circulation is possible in this way.

But now this hypothesis is not regarded valid but described as a "fantasy arising

from incorrect deduction". The old theory assumes that the blood returning from the lungs is highly oxygenated and that the blood returning from the remainder of the body is deoxygenated as such is sent directly for oxygenation. This is not altogether correct for the frog uses its lungs for breathing only under certain circumstances. While the frog is at rest the air is continually pumped into and out of the buccal cavity, through the nostrils, it is forced into the lungs only rarely. The respiration goes on in the buccal cavity, the exchange of gases taking place through the moist mucous membrane of the buccal cavity. The frog also carries out respiratory exchange through the moist skin (cutaneous respiration). Naturally the blood returned from the skin (pulmocutaneous vein) and from the buccal cavity (jugular vein) is richer in oxygen content than the blood returned from lungs by pulmonary veins. While under water only cutaneous respiration is possible and the frogs normally spend a considerable amount of time under water. Under these conditions the blood from the lung will be the poorest in its oxygen contents. Naturally the blood returned from the skin will contain more oxygen. These facts created doubt in the old theory.

The frog's heart is now regarded as a single circuit heart. As these animals breathe mainly by way of the skin and the mucous membrane of the buccal cavity, assisted by lung breathing, the oxygen obtained by the lungs is supplementary and is distributed along with the oxygen received from the buccal cavity to all parts of the body.

Some authors (Vandervael, Foxon, etc.) have recently established that the blood passes up both sides of the spiral valve in the conus simultaneously (not in two streams, i.e., first in the right part then in the left), and that the spiral valve does not change in its position during the contraction of the ventricle. Secondly, at each heart beat the blood begins to move and stops in all three main arteries (carotid, systematic and pulmocutaneous) simultaneously. Vandervael made these observations by a unique method of illuminating the heart of a 'pithed' or decerebrate frog from below, while making observation, through a suitable binocular microscope from above. Foxon confirmed his observations. Vandervael injected Indian-ink particles into the pulmonary vein and observed that passing through the heart they were distributed to all the three arterial vessels. Foxon¹ has confirmed this observation. Some other workers (Foxon and Walls) injected substance opaque to X-rays² and made radiographs at intervals. This also proved the same thing—that there is no selection of blood for the head and that the blood is pumped into all the three vessels simultaneously.

It seems that the spiral valve mainly exists for mechanical reasons. It prevents the conus arteriosus from closing altogether and also provides a degree of mechanical support to the conus which ensures that the main contraction is in its diameter and not in its length. Further by providing a rigid support it probably enables a greater blood pressure to be obtained by the contraction of the conus than would otherwise be the case. The carotid labyrinth which is believed to help in making the selection of the blood, has a different function. On the basis of some recent evidence it can be stated that the carotid labyrinth in frogs may have a function akin to that of carotid sinus in mammals. This is a sensory organ detecting pressure changes. The presence of two auricles also cannot be explained with reference to the above view. In some tailed amphibians the atrium is undivided into which both 'arterial' and venous blood is poured. There are some points, however, that need further investigations. But it is certain that there is no attempt to avoid mixing by mechanical means as suggested by the old classical hypothesis.

If there is no attempt to avoid mixing of the blood then what is the use of the pockets in the ventricular walls? It is clearly understood that the muscles of the heart themselves require plentiful supply of oxygen to carry on their work. For this work the heart is provided with coronary arteries in fishes, which run back from gills to bring oxygen directly to the heart. But the frog has a very poor coronary supply, and those who have investigated it have shown that the single small coronary artery does not supply the

¹ Foxon has introduced the use of a 'micrometer injection apparatus with the help of which very small measurable quantities of injection fluid can be put in.

² Colloidal suspension of thorium dioxide called "Thorotrast".

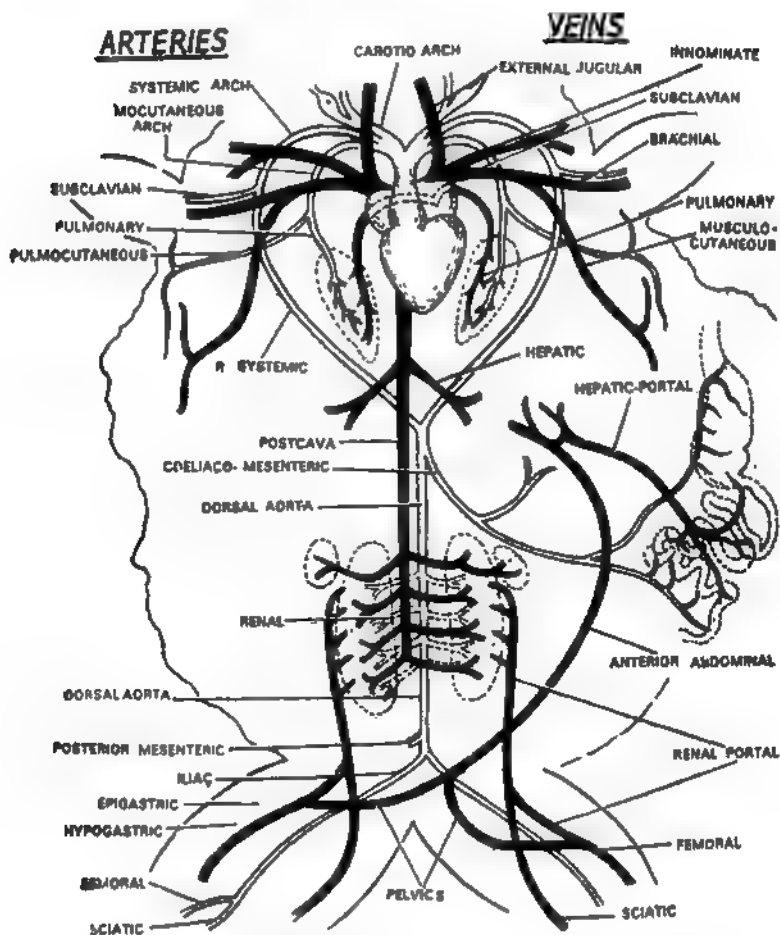


Fig. 5.28. Blood vessels of the frog.

muscles of the ventricle. The muscles of the ventricle actually get their supply of oxygen from the blood that passes through it. As the ventricular walls need more oxygen in response to a greater pumping work they have to carry on, its oxygen assimilating surface has been increased by the appearance of the pockets.

Arterial System. The arterial system begins with the truncus arteriosus which, after its bifurcation, splits into three pairs of arteries which are symmetrically disposed on either side of the middle line. Of these the anterior common carotid goes to the head, the systemic to the body and viscera, and the pulmocutaneous to the lung and skin. The common carotid divides into the external carotid and the large internal carotid. The external carotid runs forward to the tongue as such it is also called the *lingual*. *En route* it supplies branches to the thyroid gland and various muscles of the

hyoid Where the carotid divides there is an oval enlargement, the carotid gland, meant to equalize blood pressure in the vessels beyond. The carotid gland develops through the anastomosis of vessels connecting the afferent and efferent arteries of the gill-arch of the larva. The internal carotid runs forward and gives rise to a palatine artery, which supplies the roof of the mouth, a little farther it gives rise to the cerebral carotid that enters the cranium in the region of the orbit and supplies the brain, the third branch, the ophthalmic passes onward and supplies the eye and neighbouring tissues.

The two systemic arches pass outward and curve around the oesophagus to join to form a median dorsal aorta, which proceeds backward beneath the vertebral column. Each systemic arch gives rise to a small laryngeal artery, near its origin, supplying the larynx and certain muscles of the hyoid, a small oesophageal in the dorsal aspect of the oesophagus, and the occipitovertebral just behind (or common) with the oesophageal. This splits into two, a vertebral extending along the vertebral column and an occipital giving branches to the upper and lower jaw, orbit and nose. The large subclavian artery arises from the systemic arch behind the occipito-vertebral and supplies the arm. From the dorsal aorta arise a number of arteries. A large coeliaco-mesenteric artery arises at the junction of the two systemics and supplies the alimentary canal. It divides into an anterior coeliac artery and a posterior branch, the anterior mesenteric artery. The coeliac gives off branches to the left side of stomach (left gastric artery) a right gastric supplying the right side of the stomach and pancreas and the hepatic to the liver. The anterior mesenteric artery supplies the small intestine (intestinal artery), spleen (splenic), clonca and anterior portion of rectum (rectal). From the ventral side of the aorta arise four to six small urinogenital arteries supplying the reproductive organs, fat-bodies and kidneys. The aorta also gives off one to four lumbar arteries distributed to the body wall. Near the posterior end of the aorta arises the posterior mesenteric artery, a small vessels supplying the posterior portion of the rectum and in the female, the median dorsal wall of the uterus. Posteriorly the dorsal aorta divides into two large iliac arteries supplying the hind-limb. Each iliac as it enters the leg gives off a branch (epigastriovecal) which divides into a epigastric to the ventral body wall and a rectovecal to the rectum and bladder. Finally the iliac bifurcates into two, a femoral, to the skin and muscles of the anterior part of the thigh and a sciatic that enters the limb along with the sciatic nerve supplying the hind-limb. The pulmocutaneous arch runs outward and upwards giving off posteriorly a pulmonary artery to the lung and a great cutaneous branch to the skin and various other structures. Of these auricularis supplies the tympanum, thymus, lower jaw, pharynx and hyoid, etc., the dorsalis supplies the skin of the back, and the lateralis extensively distributed to the skin of the side of body.

Venous System. Each of the anterior venacava is formed by the union of three branches, the external jugular, the innominate and the subclavian. The external jugular receives branches from the tongue, hyoid, thyroid and the floor of the mouth. The innominate receives the internal jugular bringing blood back from the brain and other parts of the head, and the subcapular, bringing blood from the shoulder. The subclavian receives the brachial from the fore-limb and the large cutaneous vein collecting blood from over the side of the body and the head. The posterior vena cava arises between the kidneys and runs forward ventral to the dorsal aorta. Before opening into the posterior end of the sinus venosus it receives the hepatic veins from the liver. Four to six renal veins collect blood from each kidney and pour it into the posterior vena cava. The veins from the gonads (spermathe in male, ovarian in female) lead either directly to the vena cava or to the anteriormost renal vein.

The blood from the posterior side of the body is collected by a set of blood vessels constituting the renal portal system. Two large veins the femoral and sciatic collect blood from the leg, the femoral runs along the dorsal and anterior side of the thigh and the sciatic runs along the postaxial side of the thigh. In front of the base of the thigh the femoral divides into two, the pelvic, and the external iliac. The pelvic passes ventrally and meets its fellow from the opposite side forming the anterior abdominal vein. The external iliac passes forwards and joins the sciatic vein forming the common iliac renal

portal vein, which runs along the outer margin of the kidneys sending its branches to it. The renal portal receives the dorso-lumbar vein from the body wall. Another portal system, the hepatic portal system, collects blood from the digestive tract (stomach and intestine) through several branches and carries it to the liver, where the vein breaks up into capillaries and then the blood is collected in the hepatic veins that pour it into the postcava.

Lymphatic System. Although the blood is conveyed to the tissues by the blood vessels it is never normally liberated freely into them. The walls of the finer blood vessels or capillaries are very thin and certain portions of the fluid plasma carrying necessary material escape through them (as also do some of the white corpuscles) and bathe the tissues. This fluid is called lymph. The lymph is eventually collected up in special vessels and is returned to the general circulation through the blood vessels. These special vessels are the lymphatic vessels and constitute the lymphatic system.

The lymphatic system in the frog is very extensive. In addition to the lymph spaces of the body between the organs and also of the organs themselves, the large subcutaneous spaces present under the skin are also regarded as parts of the lymphatic system. It is due to the presence of these sub-cutaneous spaces that the skin is loosely attached to the underlying muscular body wall. But at intervals the skin is attached to the body muscles by sheets of tissue or septa so that the space is divided up into chambers on the dorsal, lateral and ventral surfaces. Where the lymphatics join the venous system pulsating vessels called lymph hearts are situated. There are two such main pairs of lymph hearts, the anterior pair beneath the transverse processes of the third vertebra opening into the vertebral vein, and the posterior pair at the sides of the urostyle, which open into the transverse connection between the proximal ends of the sciatic and femoral veins.

VOCAL AND RESPIRATORY ORGANS

In the vertebrate animals the vocal and respiratory organs are intimately associated owing to the fact that the production of sound is caused by the expulsion of air from lungs. Except the sounds made by a few fishes the voice makes its first appearance in the amphibians. In the urodeles, or lowest division of the group, the voice is, as a rule, feebly developed or entirely absent. It attains its maximum in some of the Anura.

Vocal Apparatus. The sound producing organs of the frog are located in a sort of box called the larynx situated just below the pharyngeal cavity at the beginning of the entrance into the lungs. The larynx opens into the pharynx through the slit-like glottis above and by a pair of openings behind into the lungs. It is held between the stout, bony thyroid processes of the hyoid apparatus to which it is attached by muscles as well as connective tissue. The skeleton of the larynx is composed mainly of the cricoid and arytenoid cartilages. The former consists of a slender ring surrounding the larynx and lying in nearly the same place as the thyroid process of the hyoid, to which it is closely attached. At its posterior end it is produced into a spine which extends backward between the lungs. From near the middle it gives rise to a sort of loop, the tracheal process, which is bent backward and serves as a means of attachment for the neck or roots of the lungs. The arytenoid cartilages are a pair of semilunar valves, which rest upon the cricoid cartilages. Their upper edges form the lateral margins of glottis. They afford attachment of muscle by which the glottis may be opened or closed.

The true sound producing organs consist of a pair of elastic bands, the vocal cords, extending longitudinally across the larynx. They can be seen from above by spreading apart the two sides of the glottis, or from below by removing the membranous floor of the laryngeal cavity. Sound is produced by the expulsion of air from the lungs which set the free edges of the vocal cords in vibration. Vibrations in the sound are caused by altering the tension on the cords through the action of the laryngeal muscles. The vocal apparatus of the male frog is much larger than that of the female. The males of many species of *Rana* possess a pair of vocal sacs situated at the sides of the pharynx. These sacs are out-pocketings of the pharyngeal wall which extend backward between the skin and the body. They communicate with the mouth by small openings in the floor, a short distance in front of the angle of the lower jaw. The vocal sacs are distended

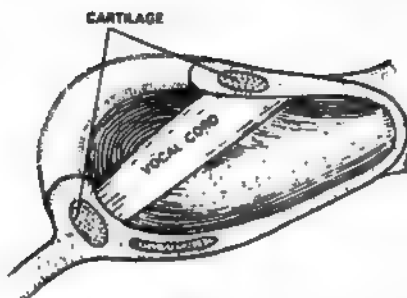


Fig. 5.29. Larynx cut open to show the vocal cord.

during the croaking of the frog through the pressure of the air in the buccal cavity. They serve as resonators to re-enforce the sound produced by the vocal cords. They are absent in the females.

Lungs. The lungs are ovoid thin-walled sacs of comparatively simple structure. They are capable of great distension and may be readily inflated through the glottis, they do not collapse when the body is cut open, owing to the fact that the glottis under ordinary circumstances remains closed. When air is let out of the lungs, they shrivel to an inconspicuous size. The inner surface of the lungs is divided by a network of septa into a series of small chambers or alveoli, by means of which the amount of surface exposed to the air is very greatly increased. The walls of the alveoli are richly supplied with blood vessels which break up to form a fine capillary network. The inner surface of the alveoli is covered with a single layer of epithelial cells which are very thin and flattened except on the edges of the septa where they become ciliated and cylindrical.

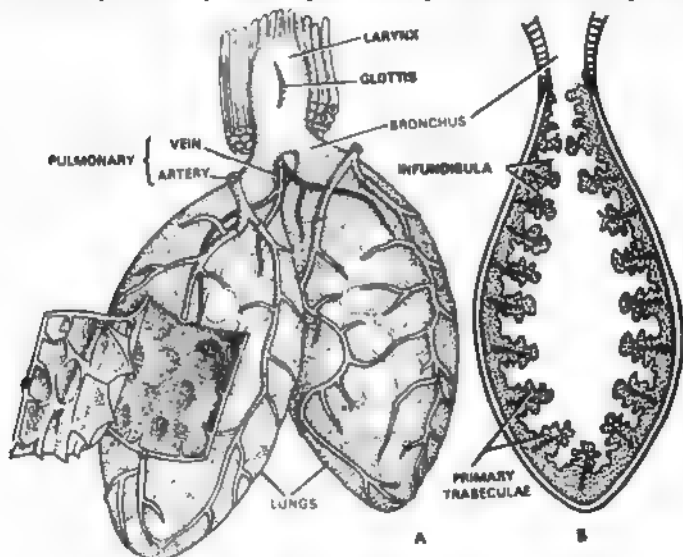


Fig. 5.30. Lateral-ventral view of the lungs of the frog.

Outside the epithelium a connective tissue layer which contains the blood and lymph vessels and numerous unstriated muscle cells, which give the lungs their great power of contraction. The outer surface of the lungs is coated with peritoneum. The area of the inner surface of the lungs of *Rana esculenta* has been carefully calculated by Krogh. In a specimen weighing 40 grams it was found to be 98 sq. cm. The total surface of the skin was estimated to be 154 sq. cm. in the same specimen.

Ventilation of the Lungs. The air is drawn in by the action of the floor of the bucco-pharyngeal cavity which actually acts as a **buccal force pump**. Ordinarily **buccal respiration** goes on in the frog. When the animal is kept quiet or where it is cool without any movement of the body, the floor of the buccal cavity is lowered by the movement of the body of the hyoid and air enters in through the open nares and as the floor is raised the air is forced out. During this period the glottis remains closed and no air passes into the lungs, the respiration taking place through the moist mucous membrane of the mouth. The air is forced into the lungs during lung breathings. This is aided by the movable maxillae situated just below the external nares. The floor of the bucco-pharyngeal cavity is lowered as in buccal respiration, air enters the cavity

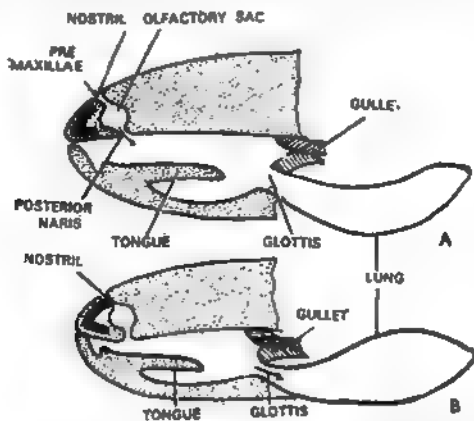


Fig. 5.31. Mechanism of respiration. A, air-getting into buccal cavity; B, into lung.

through the nostrils. Now the premaxillae are raised, the external nares closed and the hyoid apparatus is raised forcing the air into the lungs through the glottis (the gullet being closed by muscular contraction). The mouth remains closed during these activities. The drawing in of air into the lungs is called **inspiration**. Inspiration is followed by another process called **expiration**, which is effected by the contraction of the muscles of the body wall aided by the elasticity of the walls of the lungs. With the external nares closed the floor of the bucco-pharyngeal cavity is lowered and the air from the lungs is drawn into the cavity through the glottis. Finally, the glottis is closed, the external nares opened and the floor of the buccal cavity is raised forcing the air out. In the ventilation of the lungs the buccal cavity acts as a sort of force pump. The arrangement for closing the nares is an essential part of the mechanism of respiration. The frog uses its lungs only when the need for oxygen is great. The ordinary requirement is met with by the use of skin and the mucous membrane of the buccal cavity.

Cutaneous Respiration. The skin is an important organ of respiration in the frog. It becomes the only organ of respiration during winter sleep when the frog lies buried in the mud. The skin functions as a respiratory organ both in air and water. It has been found out that more carbon dioxide is given off through the skin than through the lungs. The skin has a very rich blood supply and is always kept moist, for exchange of gases through the skin is possible under moist conditions only.

The skin provides a large space that is in contact with the air for exchange of gases. The lung also does the same thing but in a complicated manner in which a large respiratory surface included in the lungs is in contact with air. These devices facilitate the exchange of gases between the air and blood. The blood contains the respiratory pigment **haemoglobin**, which combines reversibly with oxygen and acts as a carrier and it parts with oxygen when it comes into contact with tissues having a low oxygen pressure. Haemoglobin, when oxygenated, becomes scarlet, but becomes purple when deoxygenated. In the tissues the oxygen oxidises glucose (or substances derived from it) producing carbon dioxide and water and energy. In the organisms a complicated chain of oxidation-reduction reaction is involved, various substances being alternately oxidised and reduced under the influence of various enzyme-systems such as cytochrome, dehydrogenase, oxidase, etc.

EXCRETORY SYSTEM

During the process of life certain living matters as well as non-living ones break up and produce such compounds as are not helpful to the organism at all. They must be got rid of if the life is to be maintained. This process is called **excretion**. Every cell of the body assimilates, respire and excretes. Excretion is a process similar to secretion. But in this case the secretion produced is no longer useful to the animal and would, in fact, act as a virulent poison if retained in the system. It must be disposed of as soon as possible. Secretions of harmful or waste matters are distinguished as excretions.

A part of the waste is eliminated in the form of carbon dioxide through the organs of respiration. The solid products, however, cannot be disposed of in this way, hence specially suited organs are developed for this purpose. Excretion takes place in two stages, (i) discharge of waste products into the blood taking place throughout the organism, and (ii) the discharge of waste from the blood to the outside. Several organs perform this function. Less is known about such functions of skin in amphibia. Still exchange of CO_2 will take place, certain mucilaginous material is secreted that ultimately evaporates or gets mixed up with the surrounding water. In higher animals a certain amount of salt and other substances are got rid of through the sweat glands. Liver also acts as an organ of excretion. Bile is to some extent supposed to be excretion as it contains pigments produced due to the disintegration of the haemoglobin. It is through bile that waste colouring matters are disposed.

The most important organs of excretion, however, are **kidneys** which are **mesonephric** in nature. The kidneys are oval, flattened dark red bodies lying in the posterior portion of the body cavity. With the outer edge of the kidney is attached a tube, the **ureter** which developmentally is the **mesonephric duct**. It runs by the side of the kidney for a little distance and then gets embedded into it. Leaving the kidney the ducts run posteriorly till they open separately into cloacal sac. Ventral surface of the kidney is flatter than the dorsal. On the ventral surface are seen certain yellow streak the **adrenal body**.

The kidney is made up of a large number of tubes (about 2,000) bound together by connective tissue. These tubules are **uriniferous** or **renal tubules**. Each tubule has its own glomerulus lodged in the Bowman's capsule at one end and the other end opens into a collecting tubule which leads into the mesonephric duct. The kidney is supplied with blood from two different sources the renal arteries that arise directly from the dorsal aorta, and the renal portal vein which brings venous blood from the posterior portion of the body. Both kinds of vessels penetrate the substance of the kidney and anastomose forming a capillary network throughout.

Mesonephros. The mesonephros or Wolffian body is the second excretory organ to

Romer, A.S. (The Vertebrate body, 1950) does not believe that the pronephros, mesonephros and metanephros "have succeeded one another phylogenetically as they do embryologically. . . . the three appear to be regionally specialized parts of the original holonephros which serve different functions. The metanephros is a discrete formation as such it has nothing to do with pro- or mesonephros. He, therefore, calls the adult amniote kidney by the name opisthonephros, which in fact is a combined meso- and metanephros.

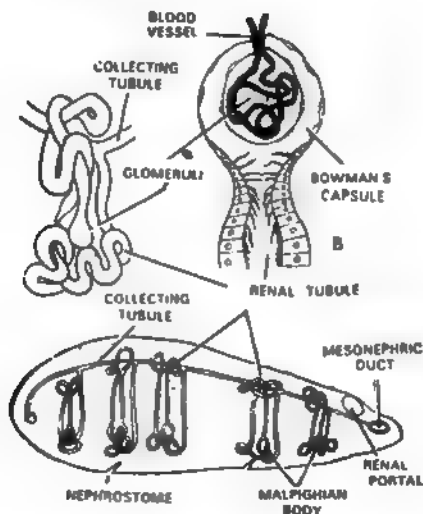


Fig. 5.32. Structure of the kidney of the frog. A, renal tubule; B, Bowman's capsule; C, diagrammatic sketch of the kidney showing the arrangement of renal tubules and collecting tubule, etc.

arise. The mesonephric tubules appear later than the pronephric tubules, arising from the more posterior nephrotomes, sometimes after a gap. They are formed exactly in the same fashion as the pronephric tubules. The mesonephric tubules are strictly segmental, at first, and continue to form along the trunk as far as the lumbar region. The mesonephric tubules differ from the pronephric in that they acquire independent glomeruli and thus are able to eliminate wastes directly from the blood vessels and not indirectly by way of the body cavity. Further the point of origin of the mesonephric tubules is dorsal to the pronephric ones and in some birds and caecilians pronephric and mesonephric tubules arise from the same nephrotome, one above the other. The mesonephric tubules become distinctly coiled. In fishes, amphibians and reptiles the peritoneal funnel, Bowman's capsule, glomerules and glandular tubes are usually typically developed throughout the series except for the first and last few rudiments which may be vestigial. At first there is but one tubule to a segment in the mesonephric region, but the segmental nature is lost by the development of additional tubules in each segment. In this way several successive generations of the tubules may be added each one being more dorsal than the last formed.

The mesonephric tubules open in the original pronephric duct (here called **mesonephric duct**) on either side. Each duct grows backwards along the lateral surface of the nephrotomes, sometimes using more nephrogenic material in its formation. In elasmobranchs and to some extent in some amphibians when the mesonephros develops, the pronephric duct divides longitudinally from its hinder end as far forward as the anterior end of the mesonephros. One of these ducts retains connections with the mesonephric tubules and forms the excretory canal. It is called **Wolffian (Leydig's) duct**. The other is **Müllerian duct** which retains connections with the pronephros and forms ultimately the oviduct in the female. In amphibians, amniotes and teleosts the pronephric duct does not divide and the oviduct is formed differently.

The function of the kidney is to eliminate waste matter from the blood. This is liquid in state and is called the **urine**, that contains many compounds in solution. Most of the

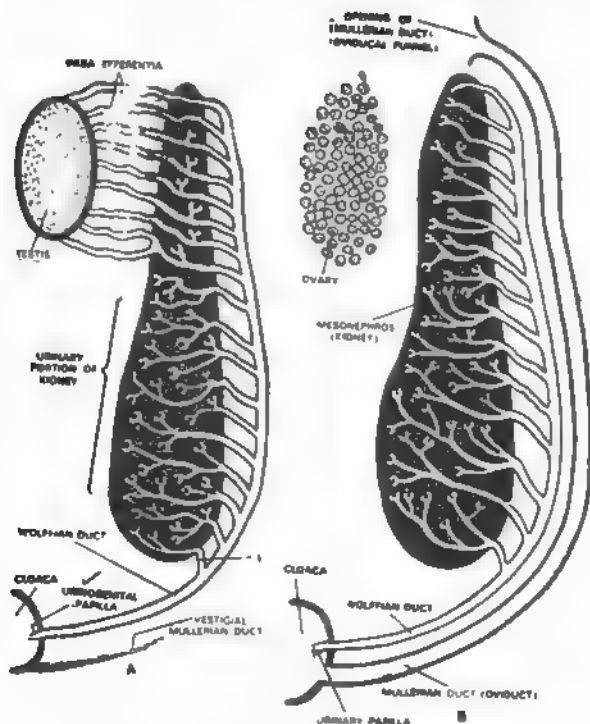


Fig. 5.33. Kidney and genital ducts in an amniote, A, male; B, female.

nitrogen leaves the body in the form of urea, $(\text{NH}_2)_2\text{CO}$, which is white crystalline compound soluble in water. Urea is the final product of the breaking down of the nitrogenous products of the body. Urea is formed in the liver. Then it passes into the blood. The tubules in the kidney extract it from the blood. The kidney also excretes several salts such as the chlorides, sulphates, phosphates of sodium, potassium,

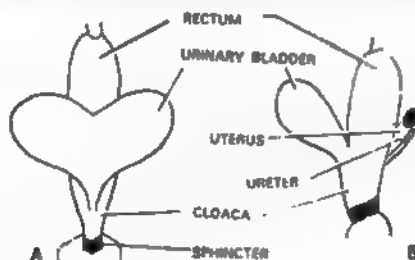


Fig. 5.34. Urinary bladder of the frog. A, ventral view; B, lateral view

calcium, magnesium and numerous other substances in small proportions. On the ventral side of each kidney are many ciliated funnels (nephrostomes) that may drain wastes from the coelom. They are connected to uriniferous tubules in frog larvae and later to the renal veins. The urine passes down the ureters to the cloaca and may be voided at once or may be stored temporarily in the thin-walled urinary bladder.

The **urinary bladder** is a thin-walled, bilobed sac attached to the ventral side of the cloaca just below the opening of the ureters. The bladder is very distensible, when entirely empty it shrinks to an inconspicuous size. It has no direct connection with the ducts of the kidneys. Generally the cloacal opening is closed by the contraction of the muscles surrounding it. The drops of urine that trickle down the ureters are collected in the bladder. The contents of the bladder are expelled suddenly by the contraction of the muscles of the body wall. The expulsion of urine often takes place when the frog leaps and also when somebody catches it.

ENDOCRINE ORGANS

The endocrine organs of the frog are essentially similar to those of higher vertebrates. The hormones formed in the frog, in general, are also of similar nature. Much work has been done, in recent decades, on endocrine system but only from the point of view of medicine and human biology. The **pituitary** of the frog is well developed and consists of usual anterior, intermediate and posterior lobes. The pituitary influences the gonads. If pituitary extract is injected it will initiate egg-laying at almost any season desired. The pituitary also has an influence on the coloration of frogs. If it is removed the darkly pigmented cells of the skin contract and the frog becomes pallid which is restored on an injection of the pituitary. The thyroid of the frog is similar in function to that of higher vertebrates or man. It has been found to be of great advantage during metamorphosis.

Little is known of the possible functions of the bodies that arise from the margins of the gill-pouches in the frog. The pancreas contains islets which are presumably a source of insulin. Frogs have tissues comparable to those which form both portions of the mammalian adrenal organs. They are different in position and arrangement. The adrenals in the frog consist of bands of yellowish tissue extending along the ventral side of the kidneys. These bands have mixed masses of cells of dual origin (corresponding to the cortical and medullary portions of mammals). The internal secretions of the sex glands are similar to those of other vertebrates, but are more restricted in their effects naturally because the reproductive functions of the frog are simpler.

NERVOUS SYSTEM

The plan of nervous system of the frog is like that of the fish. The spinal cord, the peripheral nerves and the autonomic nervous systems are essentially similar, the only noteworthy difference being that in the frog the body is so short that there are only ten pairs of spinal nerves. This number varies in different vertebrates and in man there may be as many as thirty spinal nerves. The brain of the frog, though constructed on the common plan, shows some departures.

Brain. The brain of fishes is concerned mainly with reflex activities, and there is little in their behaviour that shows anything that can be called intelligence. Their reflexes, however, are complex and more efficiently linked together (unlike invertebrates whose reflexes are simple). Not only is each part of the brain of a fish connected with a particular sense organ, such as the eye, the nose or the taste-buds or the skin, but the various parts of the brain are linked together by nerve fibres. Thus the range of its reflexes is much wider providing regular and automatic adjustments to a greater variety of conditions. At the same time the fish is not limited to purely reflex and instinctive behaviour. It can be taught to thread a maze and to change even its feeding habits. This reflects the plastic nature of an organism that appears to be a rigid bundle of reflexes. The brain in these animals, therefore, has become the agent which correlates movements in response to sense impressions.

In the frog the brain presents the first upward step in the establishment of a brain

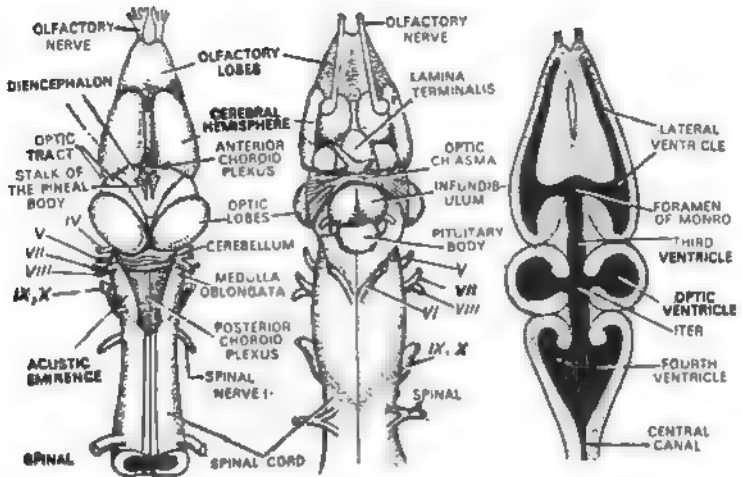


Fig. 5.35. Brain of frog. A, dorsal view; B, ventral view; C, longitudinal section of brain.

capable of "deliberate actions". In the fishes the various ganglia that form the brain are rather solid masses of cells, yet in the course of evolution they developed thin hollow outgrowths, the cerebral hemispheres, one on each side of the brain. They begin to appear in fishes, they are more developed in amphibians, reptiles and birds and in mammals they form the largest part of the brain. In the frog the hemispheres are of thin-walled pattern. The olfactory bulbs are reduced and many senses find their footing in the cerebral hemispheres. The ground plan of the brain, however, is the same and is being given below.

Fore-Brain. The olfactory lobes are small and pushed in front of the cerebral hemispheres, of which they seem to be a continuation. In between the two there occurs a shallow transverse groove. In the middle there is a definite median furrow that separates the olfactory lobes and cerebral hemispheres of the two sides, right and left. The thalamencephalon is narrower and supports the pineal body dorsally and the usual optic chiasma and pituitary body ventrally. Lobi inferiores and sacci vasculosi are absent. On its dorsal surface the thalamencephalon possesses the anterior choroid plexus. The cavities of the cerebral hemispheres are known as the lateral ventricles, which extend anteriorly into the olfactory lobes and posteriorly they communicate with the third ventricle by the foramen of Monro.

Mid-Brain. The mid-brain consists of very well developed optic lobes and the crura cerebri. The optic lobes are two prominent rounded protuberances on the dorsal side and project sideways so that they are visible from below. Ventrally the crura cerebri are hidden by the posterior part of the pituitary body. Each optic lobe has a cavity or optic ventricle communicating with the fourth ventricle behind through a narrow cavity, the iter.

Hind-Brain. The hind-brain consists of the medulla oblongata and the cerebellum. On the anterior dorsal region of the hind-brain there is a narrow transversely running ridge of nervous matter called the cerebellum. This is very small and reduced here. The medulla oblongata is simply a widening of the spinal cord. On its dorsal surface there is a triangular area of reddish brown colour in the fresh condition. This is the posterior choroid plexus. Within the medulla lies a triangular cavity, the fourth ventricle, a widened continuation of the central canal of the spinal cord. The fourth ventricle

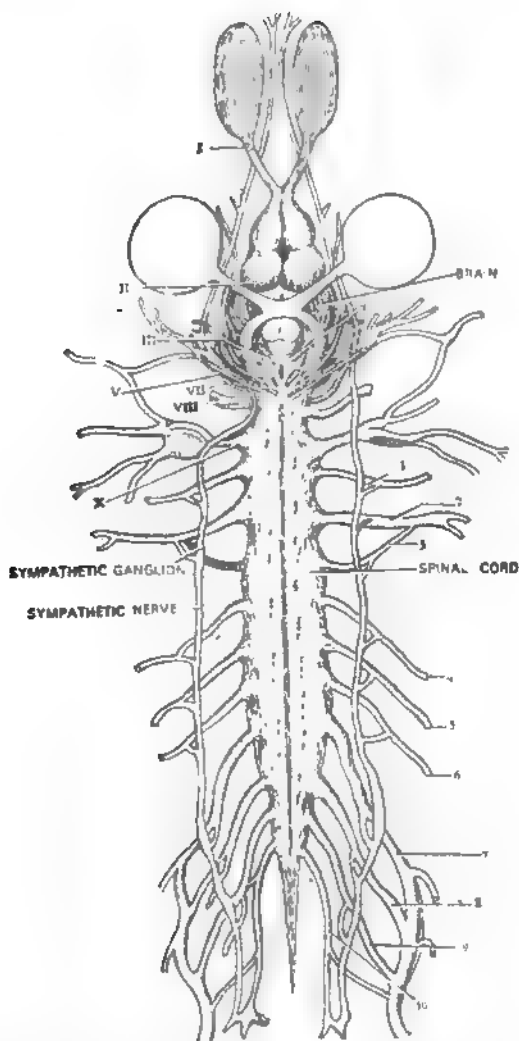


Fig. 5.36. The nervous system of frog from the ventral side. 1—10, spinal nerves; I—X, cranial nerves.

communicates anteriorly with the iter (aqueduct of Sylvius) and into it projects the posterior choroid plexus.

Spinal Cord. The spinal cord of the frog presents typical structures. It is short and somewhat flattened, and terminates in a tapering narrow thread or *filum terminale*, which extends into the urostyle. Anteriorly the spinal cord widens into the medulla. It

presents two enlargements during its course, one in the brachial region where nerves for the arms arise, and the other farther behind, where the nerve for hind legs arise. Median fissures are present both dorsally and ventrally (dorsal and ventral fissures). Spinal nerves arise by two roots, a dorsal and a ventral, at the sides of the cord. The internal structure of the cord shows that it is made up of mainly ganglion cells and nerve fibres. The central part of the cord consists of **gray matter** chiefly of ganglion cells and non-medullated nerves surrounding the central canal. At the sides it is produced to form dorsal and ventral horns or cornua. The gray matter is surrounded by **white matter** consisting mainly of medullated fibres running mostly longitudinally with isolated ganglion cells. Externally the spinal cord is surrounded by **dura matter** consisting of two layers separated by a lymph space (**interdural space**). The outer layer of this is pigmented and closely applied to the inner surface of the **neural canal** and the inner layer is devoid of pigment and lies close to the spinal cord. Within the dura mater is a thin vascular layer corresponding to the pia matter and arachnoid of the higher vertebrates.

Peripheral Nervous System—Cranial Nerves. The frog possesses ten pairs of cranial nerves. The first or olfactory nerve arises from the olfactory lobes by two roots, the anterior one emerging from the front end, the posterior running along the ventral side

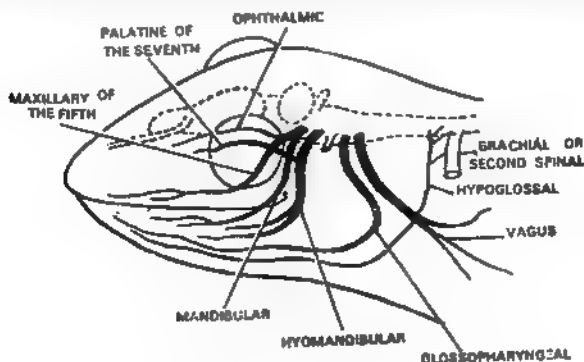


Fig. 5.37. Cranial nerves of the frog.

of the lobe nearly to its posterior end. Each nerve passes through a small foramen in the ethmoid bone and is distributed to the walls of the nasal chamber. The optic or second pair arises from the thalamencephalon, and after crossing in the chiasma, emerges from the side of the chondrocranium innervating the eyes. Both these are sensory nerves. The third or **oculomotor** is a small motor nerve arising from the crura cerebri and innervates four muscles of the eyeball (rectus superior, rectus inferior, rectus medialis and obliquus inferior). It also gives a branch to the ciliary ganglion. The fourth or **trochlearis** is also a small motor nerve arising from the dorsal side of the brain between the optic lobes and cerebellum and supplying the superior oblique muscle of the eye. The fifth or **trigeminal** is the largest of the cranial nerves. It arises from the sides of the anterior end of medulla by a pair of roots which unite in a large **prootic ganglion** before leaving the skull. From this ganglion arise two branches, the **ophthalmic** and the **maxillomandibular**, and leave the skull by a foramen in the anterior part of the prootic bone. The ophthalmic runs along the dorsal side of the orbit and is distributed to the skin of the anterior part of the head. The maxillomandibular nerve runs onward behind the eye and divides into the **maxillary superior** and **mandibular** (maxillary inferior) supplying upper and lower jaws respectively. It is a mixed nerve. The sixth or **abducens** arises from the ventral side of the medulla and emerging along with the fifth it innervates the external rectus and retractor bulbi muscles of the eye-ball. It is a motor nerve. The seventh or **facial** arises from the

medulla close behind the third and gives rise to the *palatine* to the palate that courses along the ventral side of the orbit. The second branch is the *hyomandibular* which divides into the *hyoidean* and the *mandibular* distributed in the regions of the hyoid and the jaws. It is also a mixed nerve. The *hyomandibular* cleft (spiracle) of the tadpole has, in the adult, closed up and an outgrowth from part of it has formed the tympanic chamber and the Eustachian tube of the middle ear. This changes the innervation of the seventh slightly. The *lateralis* sensory components of the seventh that were present in the dogfish disappear here and only the visceral sensory and motor elements are represented. The eighth or auditory nerve is distributed entirely to the inner ear. The distribution of the ninth and tenth nerves is completely changed in the frog because of complete suppression of the visceral clefts. The ninth or *glossopharyngeal* arises, as in the dogfish, from a number of roots in common with the *vagus*. These roots emerge from the skull through a foramen in the exoccipital, external to the condyle, and enter the large jugular ganglion. After emergence from this ganglion the *glossopharyngeal* gives a small branch to the *hyomandibular* of the seventh and then bends forward along the floor of the mouth innervating the mucous membrane of the tongue and pharynx. In dogfish it supplies the first gill-cleft. The tenth or *vagus* differs much from that of the dogfish. The branchial and the lateral-line contribution are lost, the part remaining represents only the visceral components and it gives branches to the heart, lung and stomach, etc.

Spinal Nerves. The adult frog possesses only ten pairs of spinal nerves, the number in the tadpole is much larger, the posterior ones degenerate with the loss of tail. The first spinal nerve emerges between the first and second vertebrae and its principal branch (the *hypoglossal* nerve) innervates the tongue and several muscles attached to the hyoid. The second nerve is quite large and receives a branch of the first anteriorly and third spinal nerve posteriorly forming the *brachial plexus*. The fourth, fifth and sixth nerves are small and are distributed mainly to the skin and muscles of the wall of abdomen. The seventh, eighth and ninth pass almost directly backward and anastomose forming the *sciatic (lumbosacral) plexus*. Before merging into the sciatic plexus the seventh gives rise to the *ilio-hypogastric* branch to the muscles of the abdomen. From the plexus arises the *sciatic* nerve and goes into the leg on each side. Proximal to the knee each sciatic divides into the *tibialis* and *peroneus*. The *tibialis* gives branches to the *gastrocnemius*, *tibialis posticus*, and numerous muscles of the plantar surface of the foot. The *peroneus* innervate the *peroneus* muscle, the *tibialis anticus* and the muscles on the extensor surface of the foot. The small tenth nerve receives a branch of the ninth and forms the *lacio-occygeal plexus* which gives branches to the bladder, cloaca, oviducts and posterior lymph hearts.

The *sympathetic nervous* system consists of two thread-like nerves, strands above the dorsal wall of the coelom. Each has 10 ganglia and many fibres connecting the brain, spinal cord and viscera. Each trunk receives a branch from each of the spinal nerves and where the two join there is a ganglionic enlargement. The system directs many internal functions not under voluntary regulation such as the rate of heart beat, the secretion of digestive juices, muscular movements in the stomach and intestines, and muscular tone of blood vessels.

SENSE ORGANS

Eye. The fundamental pattern of the eye is similar to that of the fish studied. The upper eyelid is a narrow, thick fold extending from the upper edge of the orbit. It has no power of independent movement, but may be raised or lowered by the movements of the eyeball. What appears as the lower lid is really made up of two elements the lower lid proper and the nictitating membrane. The lower lid consists of a lower thick portion and an upper thinner part, which is folded in behind the former when the eye is uncovered. The nictitating membrane is thin semilunar fold (Fig. 5.38) somewhat more transparent than the upper portion of the lower eyelid, from which it is separated by a slight furrow.

The closing of the eye of the frog does not occur through the independent movements of the eyelids as it does in ourselves, but is a consequence of the retraction

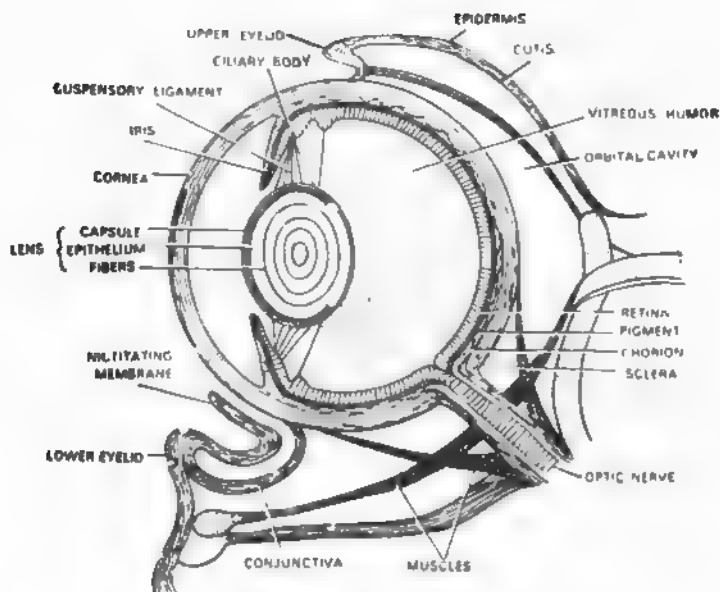


Fig. 5.34. Sagittal section of the orbit and the eye of frog.

of the eye within the orbit. A careful observation reveals that every time the lids are drawn together eyes sink into the head. Whereas the opening of the eye is accompanied by the protrusion of the eyeball.

The structure of the eyeball is similar to other vertebrates. The outer sclerotic coat of connective tissue forms a supporting case with a transparent front, the cornea. The choroid is the next layer that contains blood vessels and much black pigment to exclude all light except that entering in front. Retina is the inner-most layer containing optic receptors rods and cones that are connected to the optic nerve. Part of the choroid coat is specialised as the iris, a pigmented disc lying inside the cornea. The iris is pierced by a central opening or pupil through which light enters the spherical lens suspended by suspensory ligaments originating from the ciliary body. The space in front of the lens is filled with water aqueous humour and that behind with a jelly-like vitreous humour.

The amount of light falling upon the retina is regulated by the iris which acts as a screen or curtain, admitting the rays only through its aperture, the pupil. Near the margin of the pupil there is a ring of smooth muscle cells forming a sphincter pupillae, which causes the pupil to contract. Strong light causes a contraction of the pupil and consequently a diminution of the amount of light that falls on the retina, thus checking the excessive stimulation of the sensitive part of the eye. This is the direct effect of excessive light on the sphincter pupillae muscles of the iris since it has also been observed to occur in eyes that have been removed from the body.

The optic arrangements of the eye of the frog are such as to throw images of objects upon the retina. The sensitive layer is thereby stimulated and impulses carried through the optic nerve to the brain, there giving rise to sensation of light. The eye of the frog has no power of accommodation for viewing both near and distant objects such as our own eyes have. The lens cannot either be changed in form or brought nearer to or farther from the retina, so that only those objects are in focus which are at a particular

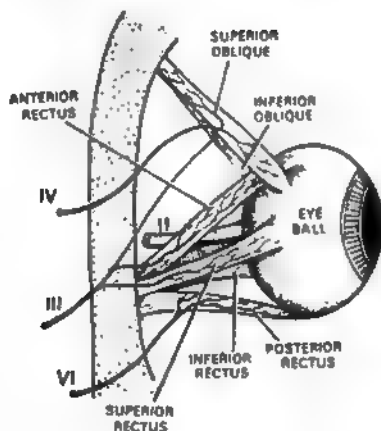


Fig. 5.39. Eye of frog, *in situ*, III, IV, VI, cranial nerves.

distance from the eye. Images of objects at other distances are not clearly outlined and there consequently results imperfect vision. In air the frog is myopic or near-sighted (Plateau, Hirschberg, Beer). It can see clearly those objects that are near at hand. The myopia of the frog is evidently an advantage to the animal in securing food, as it is important to see clearly objects sufficiently near to be snapped at. It is well known that frogs can perceive movement much more than other forms and for this purpose only indefinite and blurred images suffice. Large moving objects are taken up as enemies and hence no definite image is required for the frog to get out of the way. The frog lacks the stereoscopic depth effect, possible in higher animals.

Olfactory Sense. In the frog the distance between the internal and external nasal openings is not much, as such large nasal passages have not developed. But there are small well-developed olfactory sacs in folded fashion, which appear to furnish the frog with important sensory information as they are connected to the olfactory nerves. The olfactory cells of the mucous epithelium are very variable in form, but are usually long and narrow. What part is played by the olfactory sense in the frog is not clearly understood.

Ear. There is no external ear in the frog. The eardrum, the *tympanic membrane*, is situated on the surface. Within the eardrum there is the middle ear or *tympanic cavity* which communicates with the pharynx through the *Eustachian tube*. The tympanic cavity is crossed by a single slender bone, the *columella auris*, that transmits vibrations from the eardrum to the inner ear. The inner ear lies within the auditory capsule formed by the prootic and exoccipital bones of the skull. The inner ear or *membranous labyrinth* is a sac-like structure divisible into an upper *utricle* and lower *sacculus*, and gives rise to three *semicircular canals* embedded within the cartilage of the auditory capsule. There is an *anterior vertical canal*, a *posterior canal* and a *horizontal canal*, all three at right angles to each other. At one end each arm is furnished by an enlargement or *ampulla*. At the base of the sacculus there are four irregular pockets and from its median side arise the *ductus endolymphaticus*. The utricle, sacculus and the semicircular canals contain masses of similar crystals or *otoliths*. The internal ear is surrounded by a *perilymphatic fluid* and within the ear there occurs the *endolymphatic fluid*. The frogs do not have well-developed hearing mechanism. Instead of a well-developed cochlea there is only a small patch of sound receiving tissue. Frogs usually respond to croaks. This evidently proves that they can hear. They cannot discriminate between tones of various pitch. The system of canals

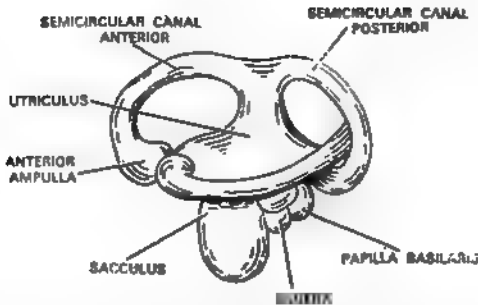


Fig. 5.40. Membranous labyrinth of frog, outer view.

and sacs in the inner ear are responsible for adjusting the equilibrium of the body as in other vertebrates.

Lateral-line System. The lateral-line sense organs are important sensory structures which enable the animal to register movement and pressure in the water around them. This provides a valuable sensory aid to the swimming animal. Such a system of sense organs is absent in the adult frog, but is present in the tadpole larva. In the development stage the tenth cranial nerve sends a growth posteriorly beneath the lateral body epidermis, on either side. It runs posteriorly to the tip of the tail. Along the cords arise groups of sensory cells which grow through the epidermis to become exposed along the sides of the body as the **lateral-line system**. The exposed cells are ciliated, and are therefore sensitive to vibrations in the surrounding aquatic medium.

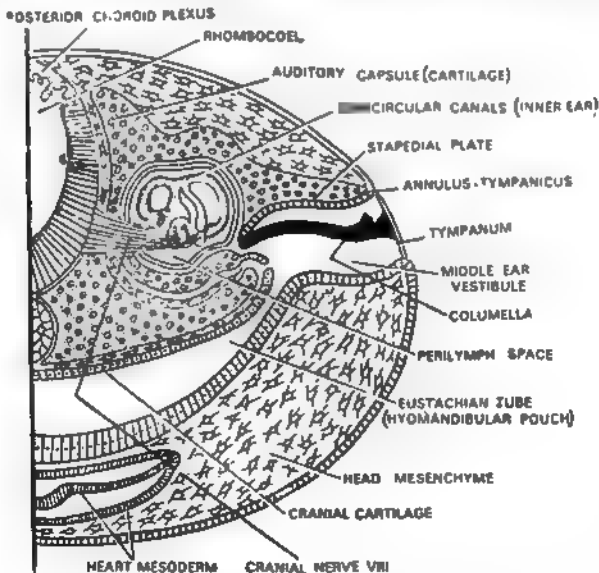


Fig. 5.41. Section of the head of frog passing through the ear region.

This system is a vestige of the aquatic ancestry, which disappears by the time of metamorphosis.

REPRODUCTIVE SYSTEM

The reproductive system has the function of producing the sex cells and transporting them outside the body. The first function is performed by the primary sex organs, ovaries in the case of females and spermaries or testes in the case of males. While the ovaries and testes are homologous organs, the sexual products are carried to the outside in the two sexes by very different methods.

THE MALE

Genital Organs. As already noted the main male genital organ that produces and discharges sex cells is the testis. The testes are whitish or yellowish cylindrical or ovoid organs longer than broad. They lie ventral to the kidney attached to the outer edge of its anteriormost portion. They are suspended by a fold of peritoneum called *mesorchium*. From the testes arise a number of slender tubes, the *vasa efferentia*, which enter the kidney. Each tubule is slender tough-walled and interbranching duct lined with closely packed cuboidal cells. Each duct is connected directly with a number (8 to 12) of Malpighian corpuscles of the kidneys by way of Bowman's capsules. These connections are permanent, so that the anterior uriniferous tubules of the kidney contain spermatozoa during breeding season. The testes produce male cells known as *spermatozoa* that pass through the substance of the kidney into the urinogenital duct. In some frogs the free portion of the urinogenital duct gets dilated forming the *seminal receptacle*. This stores the spermatozoa till such time as required.

Each testis consists of a large number of closely packed, oval-shaped sacs called *seminiferous tubules*. The spermatozoa are produced within them. They are separated

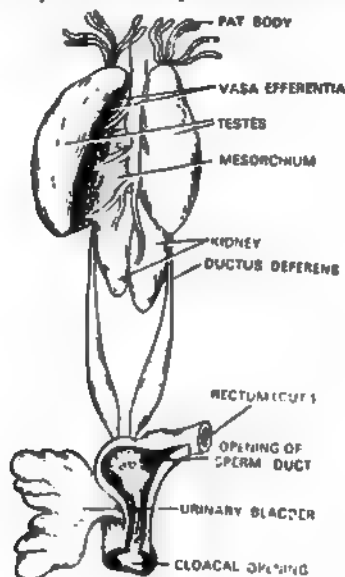


Fig. 5.42. Reproductive organs of male frog.

from each other by thin partitions (**septula**) of connective tissue called **interstitial cells**, which secrete the hormones influencing the secondary sexual characters. The thickness of this tissue is much reduced immediately after breeding. The testis is enclosed in a fibrous connective tissue capsule called the **tunica albuginea**. Each seminiferous tubule is lined with **germinal epithelium** which produces sperm-mother cells or **spermatogonia**. They keep on multiplying for some time. Shortly after this each spermatogonium enters upon a period of rest, the mitotic activity stops but nuclear activity continues. In between the spermatogonia some large cells, the **primary spermatocytes**, may be found. They are produced by the spermatogonia. They give off polar bodies and form **secondary spermatocytes**, which are smaller than the primaries and lie toward the lumen of the tubule. Following another division the **spermatids** are produced which are even smaller and possess a condensed nucleus of irregular shape. Clusters of spermatids appear as blusters of granules. The spermatids metamorphose into **spermatozoa**. The mature **spermatozoon** is about .03 mm in length, has an elongated solid staining head containing the nucleus, with an anterior **acrosome**. The short middle piece generally is not visible, but the **tail** appears as a gray filamentous extension into the lumen, about four or more times the length of the sperm head.

In any transverse section of the testis, bundles of sperm heads or tails may be cut at right angles or tangentially giving wrong suggestions about the structure. The mature sperm depends upon external sources of nutrition, so that it joins to form a congregation of 25 to 40 spermatozoa, the heads of all of which may converge into the cytoplasm of a relatively large columnar basal cell known as the **Sertoli cells**. Functionally this is a nurse-cell supplying nutriment to the cluster of mature spermatozoa till they are liberated.

Secondary Sexual Characters. The mature male is generally smaller than the female. The male possesses a slender and **streamlined** body, a **darkened thumb** which changes its colour-intensity and thickness as the breeding season approaches, and the male produces distinct low **guttural croaking** sound. In many species males show other features such as brilliant colour on the ventral surface of legs (*R. sylvatica*), black chin (*B. fowleri*) or differentiation in the colour and size of tympanic membrane.

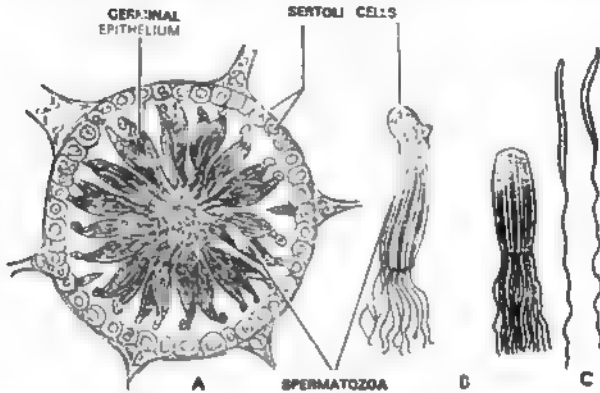


Fig. 5.43. Cross-section of testis of the frog. A, diagrammatic sketch of a lobule containing sperm bundles; B, sperm bundles; C, sperms; sketch in front of B shows acrosome on the sperm head.

Fat-body. Attached to the anterior end of the testes may be seen a yellowish organ, the **fat-body** (*corpora adiposa*). Each consists of a number of finger-like out-growths, whose number varies very greatly. Even in the same individual the number varies at different periods. The fat bodies represent stored nutrition for the long period of

hibernation and for the pre-breeding season when food is scarce. The fat-bodies consist of clusters of vacuolated cells. It is believed that the fat-bodies as well as the gonad arise from the genital ridges of the early embryo. The fat-bodies tend to be reduced soon after the breeding season, only to be built up again as the period of hibernation comes near.

THE FEMALE

Genital Organs. The ovaries of the frog are paired, multilobed organs attached to the dorsal wall of the body by a double fold of peritoneum, the *mesovarium*, which surrounds the entire ovary as *theca externa*. Each lobe of the ovary is hollow and its cavity is continuous with that of other lobes. Each ovary may contain as many as 7 to 12 lobes. The ovaries occupy the same relative position in the body cavity as is occupied by the testes in the male. The size of the ovary varies with season. In the breeding season they may fill the body cavity and may even distend the abdomen. The number of eggs varies from 2000 (*Rana pipiens*) to as many as 20000 (*Rana catesbeiana*) each measuring about 1.75 mm. in diameter (*Rana pipiens*). The mature eggs are highly pigmented on the surface of the animal pole. It is for this reason that the mature ovary presents a speckled appearance of black pigment (animal pole) and white yolk (vegetal pole). After the discharge of the ova the ovary becomes so small and pigmentless that it becomes difficult to locate it. It, however, contains oogonia for the following year.

Within the outer peritoneum the *theca externa*, are suspended thousands of individual sacs, each of which consists of another membrane the *theca interna* (or *cyst*) which contains smooth muscle fibres. The *theca interna* surrounds the entire egg except for a small area bulging towards the body cavity. At this bulge the egg is covered only by the *theca externa* and it is this region that ruptures for ovulation. Within the *theca interna* and the ovum there are follicle cells derived from oogonia. The *theca interna* plus, the limited covering of the *theca externa*, and the follicle cells

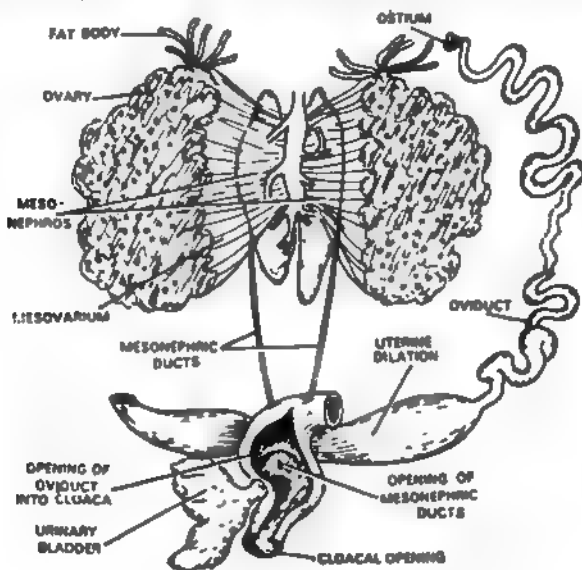


Fig. 5.44. Reproductive organs of a female frog.

form the ovarian follicle. In the ovary of the frog the ovarian connective tissue or stroma is limited very much, being represented by the two membranes, the theca externa and the theca interna. Each egg is surrounded by a non-cellular transparent vitelline membrane, probably derived from the ovum as well as the follicle cells. This membrane develops during maturation. After the egg is fertilized a fluid-filled space appears within this membrane and is called the perivitelline space. Essentially the egg is just like a large sac of yolk, the heavier and larger granules of which concentrate at the vegetal pole.

On the side of each ovary lies greatly convoluted tube of white colour. These are the oviducts and are suspended by a double fold of peritoneum. The oviducts run from below the lungs to the cloaca where they open separately. Anteriorly each oviduct opens by a slit-like infundibulum or ostium tubae, with ciliated and highly elastic walls. The body cavity of the female is almost entirely lined with cilia that beat in the direction of one of the ostia. As the ostia are produced under the influence of the ovarian hormone they are considered to be the secondary sex characters. The peritoneum covering the entire body cavity bears cilia—even that portion covering the liver and the heart is ciliated and only the surface of lungs is without cilia. These cilia produce a ciliary current directing the ova towards ostia. At the posterior end each oviduct widens out to form thin-walled very distensible uterus, which ultimately opens into the cloaca. Ovulation takes place by the rupture of the theca externa and the naked egg covered by vitelline membrane is released in the body cavity often in distorted form (they become distorted as they are literally squeezed out of a rupture of the follicle). They ciliary currents force the egg into the ostium and oviduct. As the egg passes down the oviduct by ciliary currents, it receives coating of albumen (jelly). The initial coat of jelly is thin but of heavy consistency. It is closely applied to the vitelline membrane. As the egg moves down more coatings are added. These layers are transparent and of

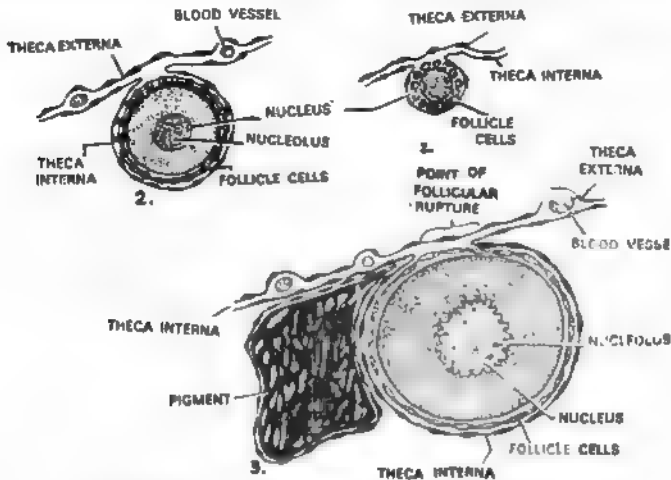


Fig. 5.45. Cross-section of the ovary of frog showing oogenesis. 3, nucleus.

uniform thickness, the jelly becomes very thick on coming in contact with water when the egg is laid. The thickness may exceed the diameter of the egg. The eggs are discharged only in the presence of the male.

Secondary Sexual Characters. The mature female frog is generally larger than the male of the same species at the same age. In the female the dark thumb pad of the male is lacking and they are not able to produce the cheek pouches as do the males. Their

abdomen is usually flabby and distended and the peritoneum lining the body cavity is ciliated. In some cases during the breeding season dermal papillae occur on the skin evidently to aid clasping by the male.

Fat-bodies. The fat-bodies (*corpore adipose*) are found in female also, but in these it is less closely attached to the gonad than in the male. In other detail the fat-bodies in both the sexes are similar and function as store-house of nutriment.

Egg. The egg in the ovary is separated from the body cavity by the thin non-vascular *theca externa* (Fig. 5.45), which is ruptured and the egg slowly emerges out of the small opening. Ovulation is brought about under the influence of some pituitary hormone, which digests the tight and non-vascular *theca externa*. Then the unstriped muscle fibre of the *theca interna* (Fig. 5.45) are stimulated (by pituitary secretion) and they force the egg out. The first maturation division occurs at the time of ovulation and the first polar body is extruded. The egg is now called the *primary oocyte* and it is in this stage that the egg is released in the body cavity. At this stage it is spherical in form (approximately 1.6 mm. in diameter). About half of its surface is furnished with a layer of pigment and, therefore, appears blackish-brown in colour. The colour of the other half is lighter and it is filled with yolk. The egg nucleus (*germinal vesicle*) is large and lies in the pigmented half, which is called the *animal hemisphere*. At a point near the animal pole the first polar body may be visible within the thin viteline membrane. The second maturation division begins soon after the first is over after extruding the first polar body, but it is not completed till the egg is activated by the sperm, as such the egg is laid in one of the stages (usually metaphase) of the second maturation division. As the egg moves down it receives a thick coat of *albumen*, secreted by the walls of the oviduct. This albumen swells up on coming in contact with water in which the eggs are laid. The albumen of the egg sticks together forming the characteristic frog *spaw*.

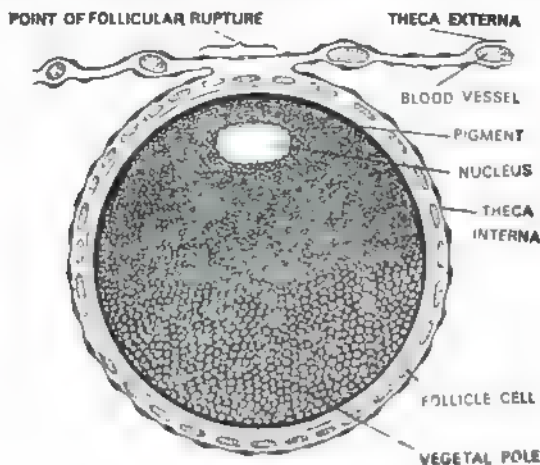


Fig. 5.46. Egg of frog ready to be released.

Copulation. In copulation the male clasps the female just behind her fore-legs where he hangs tightly and maintains his hold persistently against all efforts to dislodge him. To increase the firmness of the hold often the thumbs are interlocked, compressing the body of the female greatly. Female is responsible for locomotion, male exerting himself only to maintain the balance. This is called the *amplectic embrace* (or *amplexus*). Amplexus does not occur in all amphibians. It occurs in frogs and toads, but not in urodeles. The duration of amplexus is several days after which the eggs are

laid. The purpose of this is to pass the sperms on the eggs as soon as they are shed, for the life of the egg is very short and a quick fertilization is therefore essential.

Fertilization. The process of fertilization involves two important activities, viz., activation of the egg accomplished mostly by the sperm (sometimes by a variety of parthenogenetic agents), and mixing of hereditary (nuclear and chromosomal) potentialities (*amphimixis*). These activities follow *insemination* which simply means the exposure of eggs to spermatozoa. Fertilization in Anura is external. The female frog lays eggs in water, the male, simultaneously with egg laying, shed clouds of spermatozoa over the eggs. The jelly deposited around each egg appears to be arranged in three layers. The sperms work their way through the jelly. After one sperm makes contact with the egg surface, others do not enter the jelly and do not try to penetrate the egg. Only one effective sperm enters the egg in the animal hemisphere. The factors that limit the entry of the sperm are negative chemical and/or physical reaction of the egg toward extra spermatozoa. In case any extra sperm enters the egg it will divide independently of the egg nucleus and then degenerate. The egg nucleus fuses with only one sperm nucleus. In aged eggs many sperms have been seen entering one egg (polyspermy), but this drastically interferes with the cleavage mechanism and the egg ultimately dies. The sperm head generally makes a direct perpendicular contact with the vitelline membrane and with the help of the acrosome works its way through it. The sperm takes several minutes to enter and the tail piece may be broken off, but the head and middle piece continue through the substance of the egg in the general direction determined by the direction of penetration. Soon after entering, the sperm head enlarges, loses its identity, and its associated centrosome divides forming an axis at right angles to the sperm path. The course of the sperm is called the **penetration path**, which becomes evident because of pigment granules that the spermatozoon takes along with it from the surface layer. Frequently the egg nucleus moves away with the result that the sperm path is diverted to meet the egg nucleus. The diverted course of the sperm path is called **copulation path** because it results in the copulation (or fusion) of the two nuclei. By the time the two nuclei meet the two sperm centrosomes are ready to form the division spindle for the first cleavage.

Changes in the Egg. Egg is laid in the form of secondary oocyte, and as the fertilization occurs at once, even the albumen covering of the egg does not get time to swell up. The entry of the sperm brings about the completion of the extrusion of the second polar body. At the time of insemination the first polar body is in the form of a bean floating freely within the perivitelline space near the animal pole. Soon a second polar body is extruded through a small pit that appears close to the first polar body. At the completion of the maturation the jelly swells up to its maximum as it imbibes more and more water. Ultimately the jelly becomes arranged in three layers, the thickness of which is several times the diameter of the egg. Soon after the penetration of the sperm there is an almost immediate loss of water from the egg, so that a space, the **perivitelline space**, appears between the surface of the egg and the enveloping vitelline membrane, which is now known as the **fertilization membrane**. The perivitelline space is filled with a fluid, within which the egg is free to rotate. The egg rotates in such a way that the black pigmented animal hemisphere comes to lie uppermost and the heavier yolk-laden vegetal hemisphere is lowermost.

Symmetry. While the egg is in the ovary the arrangement of its parts is radially symmetrical about an axis (the egg axis) passing directly from the animal to the vegetative poles. The effective spermatozoon enters the egg at any point within the animal hemisphere. This may be close to the egg at any point within the animal hemisphere almost at the equator, or between these two extremes. This means that a third point is established by the sperm penetration (the other two being any two points on the linear axis of the egg). These three establish a **penetration path plane**, which is of major importance in establishing embryonic planes. At the plane, which is of major importance in establishing embryonic planes. At the moment of sperm penetration the egg loses its radial symmetry and establishes the antero-posterior axis or **bilateral symmetry** of the future embryo. The side of the animal hemisphere towards the sperm penetration is the anterior and the opposite is the posterior side of the embryo. The antero-posterior plane separates the future embryo into right and left halves.

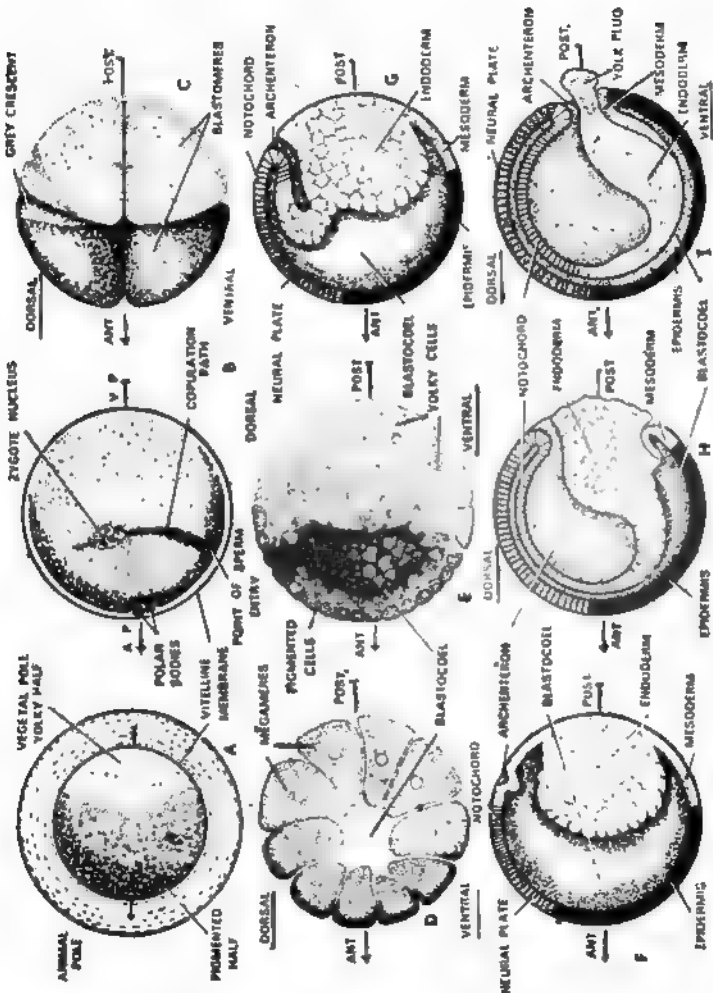


Fig. 5.47 Development of the frog. A, unfertilized egg. B, fertilized egg, 8 cell stage; C, section of early blastula. E, section of late blastula; F, (left lower row), sagittal half of early gastrula; G, later gastrula; H, I, later gastrula.

Following the invasion by the spermatozoon the egg-substance undergoes many changes, there is a streaming of protoplasm towards the animal pole and of yolk towards the vegetal pole. The minute pigment granules on the surface of the egg which appear motionless in the unfertilized egg show violent activity, and thus involves loss of pigment from the surface of the egg. As a result of this, between the animal and vegetal poles an area appears which is gray (neither white nor black). This area is crescentic in shape hence called the gray crescent, and it establishes the plane of embryonic symmetry. The gray crescent is entirely a surface phenomenon, and has nothing to do with the fusion of gametes. According to authors, who present sufficient evidence, the gray crescent has been determined before the entry of the sperm, but it simply becomes more clear after the sperm entry. In some cases the gray crescent is not readily apparent, yet such eggs develop normally (Roberts Rugh). The gray crescent marks the position of the dorsal lip of the blastopore, when it is first formed, and consequently marks the dorsal surface of the early embryo. Thus with the appearance of the gray crescent the orientation of the future embryo can be established. If two points are taken on the egg-axis and the centre of the gray crescent as a third point, this plane represents the median sagittal plane of the future embryo.

Cleavage. The egg of the frog is telolecithal, i.e., there is a large amount of yolk concentrated at one pole, opposite to the concentration of cytoplasm and the location of nucleus. The cleavages are holoblastic, i.e., total and after the second cleavage they are unequal. The first cleavage appears about $2\frac{1}{2}$ to 3 hours after fertilization. It begins as a small depression near the centre of the animal hemisphere. It appears as if some internal force is drawing the surface of the egg towards its centre. This small inverted fold gradually extends in the form of a groove until it surrounds the egg. This furrow is shallow in the beginning, but becomes deeper ultimately dividing the fertilized egg into two halves called the blastomeres. Internally the division is mitotic, thus, each daughter cell contains a nucleus derived from the copulation nucleus of the fertilized egg. This cleavage is vertical or meridional. The two cells are identical in respect of cytoplasm, pigment and yolk. The second cleavage appears about an hour after the first. The furrow of this cleavage begins at the centre of the animal hemisphere, is at right angles to the first and is vertical. This divides the egg into four blastomeres. The four blastomeres so produced are not qualitatively identical, because of these only two contain the material from the gray crescent. The third cleavage begins about thirty minutes after the second is completed or four hours after fertilization. The cleavage plane of the third furrow is horizontal and is slightly above the equator. Thus the four upper cells are a little smaller than the four lower cells. The smaller blastomeres are called micromeres and the larger blastomeres are called macromeres. The fourth cleavage follows 20 minutes after the third and tends to be vertical. This is usually a double furrow. The cleavage rate is accelerated with each of the early divisions and since the blastomeres are of unequal size and have varying amounts of cytoplasm and yolk, synchronous cleavage is lost and there is an obvious overlapping of the divisions. The uppermost cells divide more rapidly than the lowermost cells. From this point onward perfect symmetry in cleavage and in blastomeres is very rare, although the embryo develops perfectly. The fifth cleavage is also double, appearing first in the upper hemisphere and then in the lower. The cleavages thus far follow the rule¹ that each cleavage plane comes in at right angles to the previous one. The subsequent divisions become so irregular that it is impossible to trace out any plan of procedure. The segmentation continues more rapidly in the pigmented region, since at that place the protoplasm is most dense, whereas, yolk which is very abundant in the vegetal side delays cell division. The multicellular embryo at this stage is called morula by some writers (Fig. 5.47).

Blastulation. The eight-cell stage of the developing embryo shows the beginning of a cavity. This cavity is the result of segmentation, as such, it is called the segmentation cavity. As the segmentation proceeds briskly the stored nourishment is consumed and a cavity is formed. This stage of the embryo is called blastula (Fig. 5.47 D) as such this

¹ Such's law that cells tend to divide into equal parts and each new plane of division tends to bisect the previous plane at right angles.

cavity is also called the **blastocoel**. It enlarges with each of the early cleavages and is filled with albuminous fluid, arising from the surrounding fluid. Some authors prefer to call this stage **coeloblastula** (as opposed to **stereoblastula** which has no cavity). The blastocoel appears in an eccentric position, above the level of the equator (Fig. 5.47) slightly toward the gray crescent side of the dividing egg. The size of the cavity increases with the formation of more and more smaller surrounding cells. The late blastula is a hollow ball of cells.

Now the rhythmic cleavages disappear and multiplication takes irregular course. The small pigmented animal pole cells tend to spread their activity in downward direction towards the vegetal pole in such a way that there seems to be a regular migration of pigmented cells toward the vegetal pole. Further the horizontal cleavages in the very small animal pole cells give the blastula a double or multilayered roof. The single outer layer of cells contains most of the superficial pigment forming the epidermal layer which forms epithelium of the integument or lining of the nervous system. The inner layers of the cells of the roof of the blastula give rise largely to the neuroblasts of the nervous system as such are designated as the nervous layer. At the junction of the animal and vegetal pole the encroaching cells of the animal hemisphere become thickened forming an equatorial band or the **marginal zone**, where yolk is most actively being transformed into cytoplasm. Such a marginal region of activity is found in *Amphioxus* and chick, and probably in all vertebrates.

The cells of the blastula do not present much distinction in their make-up except in the degree of pigmentation, size and yolk content. There is no apparent indication as to what part the cells will play in the formation of the future embryo. Many scientists¹ have succeeded in demonstrating the ultimate fate to different cells even at the blastula stage. They have used many experimental devices, such as the vital staining, and constructed maps (fate-maps) showing the ultimate fate of various areas. This is called the **prospective or presumptive fate** of the different regions. Thus a fate-map is simply a topographical surface mapping of the blastula. The blastula is stained with various harmless dyes and the coloured areas are watched. For instance, a small area of cells stained by Nile blue sulphate (a vital dye) was picked up and watched. These cells moved from the marginal zone (between the animal and vegetal hemispheres) over the dorsal lip of the early blastopore into the embryo and became pharyngeal endoderm. The egg of the frog is very dark as such the effect of vital dyes is not clear in its case. But the fate-maps of various amphibians are basically alike (not sufficiently alike in detail), as such fate-maps of closely related species have been worked out, and giving due consideration to specific differences and the behaviour of the frog's egg in development, a reasonably accurate map of the frog blastula has been prepared. Under normal conditions the ectoderm of the frog is derived from the cells of the animal hemisphere and in part from intermediate or equatorial plate cells. These regions are designated as **presumptive ectoderm** on the fate-map. The endoderm arises partly from the intermediate zone but largely from the vegetal hemisphere area which is called the **presumptive endoderm**. The mesoderm and the notochord arise between ectoderm and endoderm, largely from the region known as the lip of the blastopore. It must be clearly understood that the limits of any particular region are not sharply defined and the fate-maps show the mean results of a number of marking experiments. It is also worth noting that with the exception of cells of the gray crescent the fate of other areas is not fully fixed or determined.

Gastrulation. This is the embryological term for the complex of cell-movements which occur in almost all animals at the cleavage period. These movements carry those cells whose descendants will form the future internal organs from their largely superficial position in the blastula to approximately their definitive position inside the embryo. If an embryo is watched from outside, the process of gastrulation appears to consist of the progressive growth of the pigmented cells over the lighter coloured yolk cells, until all the embryo is covered by the pigment cells except a small circular patch, the **yolk plug**, marking the position of the blastopore. As a matter of fact during gastrulation several complicated types of activity go on within rather simultaneously,

¹ H. A. Born, R. Humber, Speck, Vogt, Moltreuter, Nuchols, etc.

but the ultimate result is that the presumptive ectoderm comes to enclose the presumptive notochord, mesoderm and endoderm. A remarkable series of mass migrations (**formative movements**) of cells take place in gastrulation which is not caused by localised production of new embryonic material as was formerly believed. In essential the gastrulation involves a rearrangement of material already present. The cells of the embryo continue to divide actively at more or less the same rate throughout the embryo, there being no special region of "proliferation".

"Gastrulation is now recognised as an extremely complicated but highly integrated and dynamic change in the embryo, brought about by a combination of physical and chemical forces arising intrinsically but subject to extrinsic factors" (Roberts Rugh). What are the actual forces involved is not understood. Gastrulation apparently is concerned with cell-movements, changes in physical tension and in the metabolism of carbohydrates, proteins, and possibly even the lipids. The actual observable process of gastrulation is the infolding of the pigmented cells of the animal hemispheres. The cells which lies on the lateral surface of the late blastula begin to roll inwardly, first only a few cells and then, by a sort of contagion, the contiguous cells of the more lateral marginal zone. If there is any interference with this inturning movement the subsequent development is apt to be abnormal or incomplete.

Differentiation. In the case of *Amphioxus*, on completion of protoplasmic streaming after fertilisation, the fate of the different cytoplasmic regions gets fixed up and if a portion of the egg is removed then the embryo becomes deficient in some particular feature. But in the frog the cells multiply from cell areas that take on special significance on the basis of which fate-maps have been worked out. Various areas of the embryo show a new independence although they are interdependent. This change is called **differentiation**. Instead of a group of somewhat similar cells, arranged more or less in a sphere (each cell having essentially the same potentialities as any other cell) there is now a mosaic of cell groups of integrated difference. These differences are not apparent physically, but they can be demonstrated functionally and constitute the process of differentiation. If from a 2-cell embryo or early blastula of a frog embryo a lateral or a dorsal half is sliced off the embryo will readjust its growth and a normal embryo is formed, whereas, the separated ventral half either shrivels up and dies or produces ventral structures only. That is, only portions of the embryo which contain some of the gray crescent have the power of regulating the power of their development.

During normal development the various formative movements are perfectly integrated, but it has been shown by various experiments that the effects are, to a large extent, independent of one another. The changes involved in gastrulation include the following:¹ (i) Thinning of the gray crescent side of the blastula wall. From the deep layers of blastula there is a migration of cells away from the origin side of the gray crescent. This is the region where the material will be turned inward (involution), the region which will come to be known as the **dorsal lip** of the blastopore, (ii) The marginal cell zone continues to grow toward the vegetal hemisphere (epiboly), so that the cells pass below the equator. The marginal zone attains increasing rigidity so that it presses the yolk cells inward as it moves toward the vegetal pole. The blastocoel is reduced. This process has been called **pseudoinvagination** (there is no true invagination, only the cells are pressed inward). The yolk endoderm cells towards the gray crescent side separate from the epiblast forming a slit-like space (sometimes called **gastrular slit**) between the yolk endoderm and the epiblast, (iii) Then there is the initial turning or **involution** of a few cells at the lower margin of the original gray crescent, followed by the lateral extension or the invaginated space along the epibolic marginal zone. The invaginated region becomes the **dorsal lip** of the blastopore. The marginal zone cells separate from the more ventral and lighter coloured yolk cells. The cells that involute maintain their continuity with their neighbours. Thus, an infolding begins at one point but continues around the marginal zone. (iv) The cells of the animal pole continue to grow (epiboly continues), so that the portions of the marginal zone meet from all sides leaving the cells of the vegetal pole exposed within a ring of involuted marginal zone cells and are called the **yolk plug**. The cells of the pigmented marginal

¹ According to Rugh (1951).

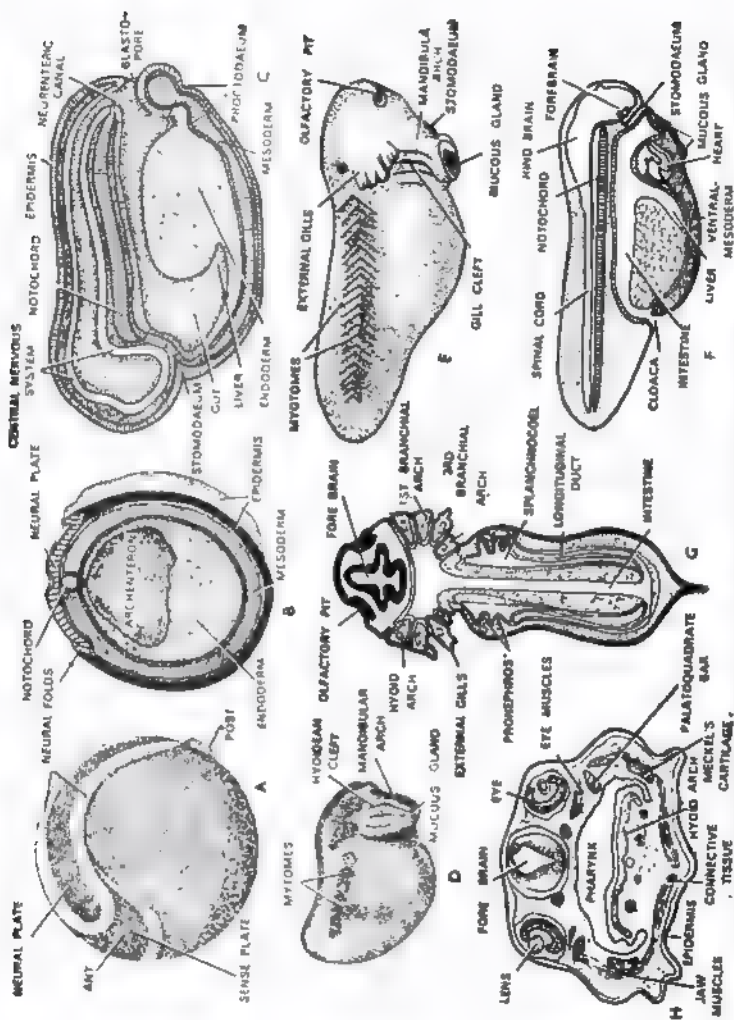


Fig. 5.48. Further stages in the development of the frog. A, early neurula; B, anterior half of neurula; C, sagittal half of late embryo; D, entire embryo, lateral view; E, larva on hatching; F, longitudinal section of larva; G, horizontal section of larva; H, transverse section through head of tadpole.

zone from the blastoporal lips of which there are four, one dorsal, two lateral and one ventral, of course they are not clearly demarcated. (v) Further epiboly of the marginal zone first makes the yolk-plug look round, then vertically oval and finally the lateral lips of the blastopore approach each other to form a vertical slit as the yolk-plug is closed over and disappears. (vi) From invaginated dorsal lip cells arises a second layer of cells, the endoderm. The sheet of cells fans out within the embryo forming a new cavity, the archenteron which gradually increases in size pushing the original blastocoel to obliteration. (vii) Simultaneously the origin of the inner layer of endoderm takes place. Some cells are proliferated off into the gastrular slit between the roof of the archenteron and the dorsal epiblast, which cells will form the notochord. Before differentiation these cells are called *chorda-mesoderm*. Since the lips of the blastopore are circular, this proliferated mass of cells also becomes circular. The more lateral and also the ventral pieces become the *mesoderm*, the dorsal one is the notochord.

The cells of the roof and lateral wall are more pigmented than the cells of the floor of embryo. The intumed endoderm surrounds the archenteron which enlarges rapidly, cause the overlying ectoderm to thicken and the whole embryo becomes elongated in. Further the presence of archenteric roof and the *chorda-mesoderm* cells above it cause the overlying ectoderm to thicken and the whole embryo becomes elongated in an antero-posterior direction, the yolk-plug marking the posterior region of the future embryo. The thickening becomes the *medullary* or *neural plate* and imparts definite antero-posterior axis to the embryo.

According to the old view the primary germ layers are ascribed particular powers under the influence of which they give rise to different organ-systems of the animals. But modern work disproves this view. The distinction of germ layers, the ectoderm, mesoderm, and endoderm is purely a matter of convenience. They have their particular fate in development not by virtue of any particularly endowed power, but by their position in the embryo as a whole. It is now clearly understood that both the endoderm and mesoderm arise from the ectoderm. This means that all these layers are fundamentally similar. Apart from this it is now possible to demonstrate experimentally that the presumptive germ layers are interchangeable. For example, the region ordinarily destined to become brain (ectoderm) may be transplanted to another region of the blastula where it may produce muscle (mesoderm) or to another place where it may become thyroid (endoderm). Thus, the germ layer distinctions depend upon their position in the developing organism. So far as the position is concerned when gastrulation is completed the ectoderm is always the outermost layer, the endoderm the innermost and the intermediate layer is mesoderm. Under normal conditions the ectoderm gives rise to the epidermis and to epidermal structures, to the nervous system and sense organs, to the stomodaeum and proctodaeum. The endoderm is the group of cells that normally gives rise to the lining epithelium of the entire alimentary tract and all its outgrowths such as the thyroid, lungs, liver and pancreas, etc. The *mesoderm* normally gives rise to the skeleton and connective tissues, muscles, blood and vascular systems, to the coelomic epithelium and its derivatives and to most of the urinogenital system. In the frog the notochord is derived simultaneously from the mesoderm and probably from the dorsal lip epiblast.

Neurulation. Surface changes. Neurulation is the formation of the neural tube. Its first indication is the neural plate which extends from the dorsal lip of the blastopore in an anterior direction as a median band of thickened ectoderm. Anteriorly it widens where the brain has to develop. Soon the lateral margins of the neural plate thicken to form the lateral (neural) folds and anteriorly they continue as the transverse neural folds. This is followed by the appearance of a longitudinal depression or neural groove in the centre of the medullary plate. The embryo becomes elongated and the medullary plate provides slightly elevated dorsal surface. The embryo is called *neurula* at this stage when the primary nervous structures are being formed. The medullary folds grow toward each other and first make contact at a point slightly anterior to the centre of the medullary plate. From this initial point of contact the medullary folds come together and fuse in both an anterior and a posterior direction. Thus the open groove is converted into a closed canal or *neurocoel* and the tube enclosing it is called the *neural*

tube. As the fusion begins in the middle it occurs last at the extremities. Thus anteriorly the tube remains open and the opening is called the **neuropore**. The posterior opening is the **blastopore**. At the posterior end the medullary folds merge into the sides of the blastopore and as the folds meet they cover over blastopore and the enteron no longer opens to the exterior (by way of the blastopore), but into the posterior end of the neurocoel. The canal connecting the neurocoel and the enteron is called the **neurenteric canal** (Fig. 5.47C).

As the neural folds fuse and the neurocoel separates from the dorsal ectoderm, the latter becomes a continuous sheet of cells above the middorsal line. The neurocoel is lined with ciliated and pigmented ectoderm and occurs as the much reduced **central canal** of the spinal cord and the brain. Slightly ventral to the anterior end of the closing neural folds there appears a semicircular elevated ridge of ectoderm, its two extensions merging with the lateral limits of the transverse neural fold. This is the **sense plate** that contains material of the fifth and seventh cranial nerve ganglia, and gives rise to the mandibular (first visceral) arches (from the mesoderm contained in the ridges), lens of the eyes, nasal placodes and oral suckers. The suckers are paired larval organs that become glandular and form adhesive mucous secretion, which the larva uses to adhere to objects after hatching.

Soon a vertical groove (**stomodaeal cleft**) appears on the anterior median surface of the sense plate. This separates the two **mandibular ridges** (arches) or the primordia of the jaws (both right and left). The ventral limit of the groove represents the ectodermal invagination called **stomodaeum**, which ultimately breaks into the pharynx forming the mouth. It is for this reason that the part of the mouth formed by the stomodaeum is lined by ectoderm. The dorsal limit of the vertical groove becomes the hypophyseal invagination. A bulge (bulbous outgrowth) appears on each side of the anterior part (head) of the embryo directly dorsal to each oral sucker. These are external indications of the internally enlarging **optic vesicles**.

Another pair of elevations appears parallel to the posterior side of the sense plate. These are the **gill-plates** that give rise to the external gills for aquatic respiration in the tadpole. It develops vertical furrows which separate the bulge into three vertical thickenings or **branchial arches**. Considering the mandibular arch as the first, six visceral arches arise normally. The first arch forms the jaws, the second or the hyoid arch forms the hyoid apparatus and the third arch forms the first pair of external gills. All the arches fourth to sixth form external gills of which the fourth is rudimentary. The arches that form the external gills are known as the **branchial arches**. Three or sometimes four of the vertical furrows open through the pharynx as clefts functioning in gill-respiration. It must be borne in mind that all arches are visceral and are numbered from the anterior side while the third visceral arch is called the first branchial because it gives rise to the first external gill.

A slightly elongated swelling appears posterior to the dorsal limit of the gill-plate. This indicates the formation of the **pronephros** underneath. More posteriorly, and slightly dorsal to this level may be seen the L-shaped surface indications of the internal mesodermal **myotomes**.

After the blastopore is completely closed a new pit-like invagination develops just ventral to the blastopore. The ectodermal invagination is called **proctodaeum**, the primordium of the anus. The proctodaeum grows deeper and deeper finally opening into the archenteron. This establishes a new ectoderm lined opening into the hind gut. The laterally compressed body of the neurula develops a bulge on the ventral side. After the closure of the blastopore tissues dorsal to it grow backward forming a **tail bud**. As the latter elongates it develops both a dorsal and a ventral fin.

Internal Changes. With the closure of the neural folds numerous surface evaginations and invaginations appear, indicating internal changes. The neurula develops cilia on the surface which tend to rotate the embryo within the fertilization membrane and its surrounding jelly.

The major part of the nervous system is derived from the original nervous layer of ectoderm. The central canal is lined with ciliated and pigmented cells. The floor and roof of the neural tube are relatively thin but the lateral walls are very thick. While the neural folds fuse some of the nervous layer, at the level of the dorsal fusion, is cut off on

either side as **neural crests**. The neural crests are actually parts of the neural folds which are not used in the formation of the neural tube. The paired neural crests extend the full length of the central nervous system dorso-laterally and will give rise to various ganglia of the central and sympathetic nervous systems, medulla of the adrenal and to chromatophores. The central nervous system is covered by reconstituted ectoderm. Owing to the spherical condition of the gastrula the anterior region of the neural tube curves ventrally at about the level of the future mid-brain and this curvature (**cranial flexure**) persists and is a characteristic of all vertebrates. The neuropore finally closes.

Now the anterior part of the neural tube becomes constricted at certain levels and the walls begin to differentiate. After some time three primary parts of the embryonic brain are limited. These divisions, known as **prosencephalon** (fore-brain), **mesencephalon** (mid-brain) and **rhombencephalon** (hind-brain) are present in all vertebrates. The fate of these portions has been dealt with earlier.

Gut (Endoderm) The anterior portion of the archenteron expands both ventrally and laterally beneath the notochord and infundibulum of the brain forming ultimately the foregut and its derivatives. At this stage the midgut is simply the tubular archenteron dorsal to the mass of yolk endoderm. That portion of archenteron found in the neighbourhood of the temporary neural canals is the hindgut. The foregut gives rise to a median antero-ventral evagination. The oral evagination, which meets the stomodaeal invagination of the head ectoderm, finally breaks through as the mouth. The large cavity of the foregut is the **pharynx** which gives rise to lateral endoderm-lined visceral pouches. Of these the most anterior one is the **hyomandibular pouch** because it comes to lie between the mandibular and the hyoid arches. The next three are the **first, second and third branchial pouches**. These extend outward toward the ectodermal invagination (visceral grooves). The foregut also gives rise to a medioventral posteriorly directed outgrowth, the **liver diverticulum** which extends a short distance underneath the yolk, and gives rise to the liver, the gall-bladder and the bile duct.

Axial Skeleton. The notochord develops from the cells indistinguishable from the mesoderm at the region of the dorsal lip. Very soon these cells enlarge and become vacuolated, and retain this nature till the notochord is replaced by the bone of the vertebral column. The entire notochord soon after its formation, becomes enclosed in an outer elastic sheath and inner fibrous sheath both of which are derived from connective tissue.

Derivatives of Mesoderm. In the frog embryo the mesoderm is in the form of sheets of loose cells extending in all directions from the lips of the blastopore. The mesoderm in the head and pharyngeal regions, is in the form of mesenchyme (loosely dispersed).

Arches. The mesoderm concentrates on the side of the pharynx in the form of vertical concentrations called the **visceral arches**. The most anterior of these is **mandibular arch**, anterior to the first endodermal pouch and ectodermal groove. This arch is associated with development of the muscles of the jaws. The **hyoid arch** is the next lying posterior to the mandibular arch. Between these develops the **hyomandibular pouch** that never breaks through to form the cleft. Posterior to this develop the **first mesodermal branchial arch**, corresponding to the first endodermal branchial pouch, the **second branchial arch** corresponding to the second branchial pouch and so on.

Somites. The mesoderm posterior to the pharynx condenses on either side of the notochord in the form of an inverted horse shoe around the archenteron and the yolk. The part of this mesoderm that lies on the sides of the notochord is the **segmental plate** and the ventral part is called the **lateral plate mesoderm**. Soon this mesoderm differentiates into a **dorsal somite mass** (**epimere**); an **intermediate cell mass** (**mesomere**) and a **lateral plate** (**hypomere**). Of these the epimere is divided into portions called **metameric somites**. The first somite appears on the anterior side and the others follow in a sequence, for this reason the anterior somites are more differentiated. The somites separate from the ventral portions of the mesoderm and take the form of blocks of cells within each of which a cavity, the **myocoel**, develops. The myocoel is not in the centre but displaced towards the lateral margin, which becomes thinner and is called the **dermatome** (cutis plate) and gives rise to the dermis

and appendage musculature. The inner layer of somites or **myotome** gives rise to skeletal muscles of the back and body. A few scattered cells may be seen between the myotome and the notochord. They are the **sclerotomes** and bud off from the somite. They give rise to the vertebral column.

The mesomere and hypomere retain their connection. From the dorsal border of mesomere develops an antero-posterior band of mesoderm, the **nephrotome**, which gives rise to the larval and adult kidneys. The nephrotomes soon become hollow developing **nephrocoel** within. They later give rise to tubular outgrowths on the side which move, sideways and backward finally uniting into a longitudinal duct. This is the beginning of the **pronephros** or head kidney with tubules as excretory agents and longitudinal duct as pronephric duct emptying into the cloaca.

The **hypomere** (or lateral plate mesoderm) splits dorso-ventrally separating the mesoderm into two layers, outer **parietal** or **somatic** layer and inner **visceral** or **splanchnic** layer. The somatic mesoderm in conjunction with the adjacent body ectoderm forms the **somatopleure** that gives rise to the skin, with its blood vessels and connective tissue. The splanchnic mesoderm in conjunction with gut endoderm forms **splanchnopleure** which forms the lining epithelium, muscles and blood vessels of the entire mid- and hind-gut. The space between these two layers forms the body cavity or coelom. In each segment two such cavities appear first, one on each side, eventually they meet ventrally forming a single visceral or coelomic cavity. The notochord interrupts the junction of the lateral plates. Between the roof of the gut and notochord lies a rod of pigmented cells the **subnotochordal** or **hypochordal** rod. Presumably this represents a vestige of connection between the endoderm (gut) and the notochord at the time of their simultaneous origin.

The lateral plate mesoderm extends into the head, ventral to the pharynx, as mesenchyme, which becomes organised into sheets that form part of the heart. As the lateral plates split in the body region, there is an extension of the split into the developing heart mesoderm. This split in the heart region forms the **pericardial cavity**. The outer layer of the mesoderm (extension of somatic layer) forms the **pericardial membrane** (**pericardium**); the inner layer (extension of splanchnic layer) forms the **myocardium** (heart musculature). Like the coelom the pericardial cavity also arises as bilateral cavities which fuse to form a single pericardial cavity surrounding the developing heart. Certain scattered cells of mesodermal origin form the lining of the heart or **endocardium**. The cells run into a sheet that rolls to form a tube enclosed by the bilateral folds of myocardium.

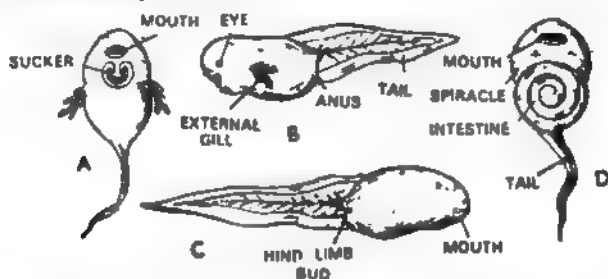


Fig. 5.49. Newly hatched larvae. Earlier larva A, ventral view; B, side view; Late larva C, side view; D, ventral view.

Larva. As the internal changes are going on the embryo shows continuous external changes. After the yolk mass forms the ventral bulge in the belly region, the pronephric and gill-bulges also become prominent. Dorsally and slightly laterally to the stomodaeum appear the olfactory pits. From the upper level of the first and the second branchial arches the external gills begin to appear.

The embryo hatches when it is about 6 mm. long. The interval between fertilization

and hatching depends upon temperature of the environment. It is believed that the hatching is accomplished by the help of temporary glands in the region of the sucker. Probably these glands secrete an enzyme under the influence of which the jelly is dissolved providing for the escape of the larva. Even after hatching the larvae are seen attached to empty jelly capsules, but the larvae do not eat jelly. Before hatching the embryos show constant swimming movements because of cilia on the surface. The embryos also show considerable muscular movements which continue even after hatching. Occasionally the larva (tadpole) may coil and exhibit S-shaped body contractions which are exclusively muscular.

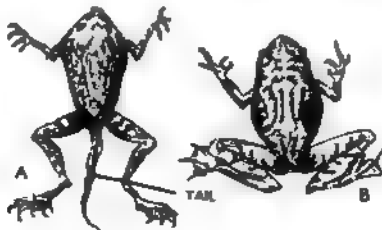
Soon after hatching the larva needs respiration. As such the developing external gills in association with the first and second branchial arches (third and fourth visceral arches) become finger-like out-growths and start respiration. The third branchial arch (fifth visceral arch) forms the rudiment of such a gill. By now the mouth also opens allowing a constant current of water into the pharynx. This water passes out through the second and the third branchial clefts (fourth and fifth visceral clefts), and over the associated external gills. The thin-walled covering of the gills is highly vascular and exchange of gases takes place through it. Subsequently the tadpole develops a set of internal gills. Now the hyoid arch produces a posteriorly directed flap like membrane, the **operculum**, covering the external gills. The opercular flaps extend ventrally and fuse enclosing the gill or opercular chamber. On the left side of the head the operculum remains open (*spiracle*) allowing entry of water. The mouth is surrounded by a pair of **horny jaws** and lips covered by **horny-rasping papillae**. The rasping papillae consist of rows of teeth-like horny denticles which are replaced frequently. They are derived from the corneum.



Fig. 5.50. Full-fed larva. The fore-limb is emerging out of the first gill opening.

As the larva begins life in the water the yolk is consumed rather rapidly making feeding necessary. With the help of oral accessories the tadpole starts feeding on vegetation. The intestine, developed from the mid gut, is a long, thin, coiled tube having the appearance of a watch spring. It is visible through the thin wall of the abdomen. The larval gut is very long. If taken out and stretched it measures nine times the length of the body. The tadpole grows in size and becomes carnivorous according to some authors.

Metamorphosis. After leading an active free-swimming existence for some time the tadpole larva undergoes a series of rapid changes transforming ultimately into a terrestrial tail-less frog. The process of rapid transformation from larval to adult form is known as **metamorphosis**. The tadpole reaches metamorphosis under normal



conditions of temperature, in about 75 to 90 days. The following are the major changes during metamorphosis (i) The lung-type (pulmonary) of respiration takes over from the internal gill phase which had replaced the external gill-phase earlier. The gill-clefts are all closed. (ii) The horny jaws are lost, the mouth widens and the gut shortens to about two or three times the length of the body. In response to the change of diet the histology of the gut also changes. (iii) Two pairs of legs develop and the tail is lost by regression. The hind-limbs arise first just before metamorphosis and the fore-limbs emerge just before the coming out of the tadpole from water. (iv) Some endocrine glands function actively and the definitive gonads appear. (v) The larval skin is shed. (vi) The mouth becomes a large horizontal slit instead of simple oval opening. Thus a frog in miniature is formed.

Economic Importance. Frogs and toads destroy a large number of insects and maintain a balance of Nature. They destroy insect pests of the crops and help the farmer. Pack (1922) has reported a case where the toad was of real value in fighting an outbreak of sugar-beet webworms. In the paddy fields of China, Japan and India, frogs have been found to occur in large numbers, undoubtedly they destroy a large number of insects harmful to the crop. In many parts of the world frog's legs form a staple food. In United States of America alone nearly a million frogs are killed each year for this purpose. Attempts have been made to establish "frog farms" but with no success so far. *Rana pipiens*, *R. catesbeiana* and *R. palustris* are the species consumed as food. In China frogs and toads are dried and sold as food. In Mexico the axolotl is used as food. Dried salamanders are used as vermifuge in Japan. In Japan and some other countries skin of toad is used as a source of fine leather.

Frogs and salamanders are universally used in the laboratory for the elementary course of Biology. They are also used for research in Physiology and Pharmacology. The larvae of amphibians afford excellent material for the study of many problems of embryology and endocrinology.

Many superstitions have been attached to frogs and salamanders. In parts of South China, the brilliant *Polypedates dennysi* is worshipped by a cult and carried about in a chair by faithful members of the group (Pope, 1931). A toad-shaped amulet from near the river Nile is dated at 3400 B.C. and a Chinese sacrificial vessel in the form of a toad belongs to an ancient dynasty (2205 to 1122 B.C.). These indicate the role frogs and toads played in religion. Aesop (560 B.C.) included frogs among his fables and Aristophanes (448-380 B.C.) dramatized their croaking choruses.

Fossil Amphibians. The first amphibian fossil has been found from the late Devonian of Greenland. The skulls of these measure 6 to 8 inches, naturally these amphibians (*Ichthyostega*) were of quite a large size. This is the period when the development of the early fish groups was at its height. They possibly have been derived from the crossopterygians and had both aquatic and aerial respiration. By the Carboniferous time, with its coal swamps, there were three distinct orders of the amphibians. These were still of the very primitive sort. They measured from a few inches to 15 feet long. They had long slim bodies, well-developed tails and possessed many internal features that indicated that they were not far from the lobefinned fishes. Only the limb capable of locomotion on land formed striking difference. The skulls of these old forms were completely covered by an armour of bone, just as in their fish ancestors, and the older amphibians are very often called Stegoccephala or 'roof-headed' amphibians. Before the Carboniferous ended, the reptiles had already appeared from the primitive amphibian stock, and towards the end of the Palaeozoic amphibians rapidly decreased in numbers. A few large degenerate remnants of the old amphibian groups survived into the Triassic but then became extinct. The salamanders appeared in the Cretaceous and were distinct from the earliest frog that appeared in the Jurassic.

CLASSIFICATION

The class Amphibia (Gr. *amphi*, dual+ *bios*, life) or Batrachia includes the animals that live partly in fresh water and partly on land. Both in structure and function they stand between the fishes and reptiles. In all the living forms the skin is moist and glandular with no external scales. No paired fins are present, instead there are two pairs of limbs for

walking or swimming (no limbs in caecilians, no hind limbs in Sirenidae). Toes are 4-5 or fewer with webbed toes of the hind limbs. Median fins lack fin rays. Two nostrils connected to the mouth cavity are present. They are valved to exclude water. Eyes often with movable lids. Ear drums external in frogs and toads. Mouth usually with fine teeth and the tongue is often protrusible. Skeleton is largely bony. Skull with two occipital condyles and ribs, if present, not attached to the sternum. Heart is three chambered with (1 or 3) pair of aortic arches and the oval red blood corpuscles with nuclei. Respiration takes place by gills, lungs, skin or the mouth lining, all together or separately. Gills are present in some stage in the life-history and in the frogs and toads vocal cords are also present. Brain with ten pairs of cranial nerves. The animals are cold-blooded—the body temperature variable, dependent upon environment. Fertilization internal or external. Mostly amphibians are oviparous.

The amphibia include the living salamanders (subclass Urodela), the toads and frogs (subclass Anura), the limbless caecilians (subclass Gymnophiona) and various fossil forms of Carboniferous and Permian time. About 2,500 living species are known. They are divided into four subclasses.

Subclass and order 1. *Stegocephalia. Extinct, from Devonian to Trias. The endoskeleton is very massive and there is an exoskeleton of bony scales. The skull has complete casing of membrane bones which are deeply sculptured. The subclass is divided into four separate orders (*Labyrinthodontia, *Phyllospindylia, *Lepospondyli, *Adelospondyli) but none appear to be likely ancestors of modern amphibia.

**Ichthyostega*, **Eogyrinus*, **Eryops*, **Capitosaurus*, **Branchiosaurus*, **Dolichosoma*, **Lysorophus*.

Subclass and order 2. Urodela (Caudata). Scaleless Amphibia with a well-developed tail which assists in the progression of the animal. The eyes are small, sometimes functionless and without lids, except in Salamandridae. Tympanic membrane and tympanic cavity are not developed. Vertebral column is long and vertebrae are opisthocelous. These are usually oviparous and mostly aquatic.

Suborder 1. Proteida. The Urodela in which the body is depressed and the tail provided with a fin. The larval gills persist throughout life in the form of three plume-like appendages on either side. No eye-lids are present; lungs present. They are permanently aquatic.

1 *Necturus* (family Proteidae). Water-newt or mud-puppy. It is 12 (or 17) inches long rusty brown amphibian with blackish spots having two gill openings, eye-lids

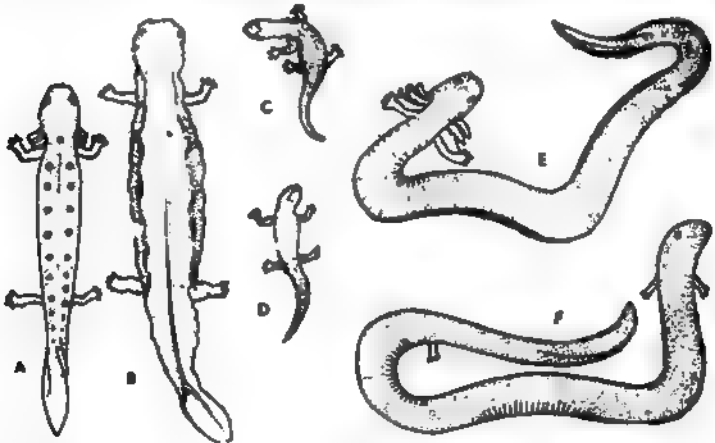


Fig. 5.52. Different types of urodeles. A, *Necturus*; B, *Cryptobranchus*; C, *Amblystoma*; D, *Plethodon*; E, *Siren*; F, *Amphiuma*.

absent, fore and hind-limbs present, fingers and toes four, trunk elongated and is separated by a slight constriction from the depressed head and passes insensibly into the compressed tail which is bordered by continuous median fin-rays. Eggs laid in "nests" attached individually by jelly-stalks to submerged stones and guarded by females. North America.

2. *Proteus* (Fig. 5.52). With three fingers and two toes, eye hidden beneath the skin; tail provided with a caudal fin unsupported by fin-rays. Rest as in *Necturus*. Inhabits the Carniola subterranean waters, America.

Suborder 2. Mutabilla. True salamanders. Larval gills disappear in the adults (except in *Amphiuma*); lungs present (except in *Plethodontidae*) and the skull is with paired vomers. There are several families. Examples of a few are given below.

1. *Amphiuma* (family *Ambystomidae*). Body eel-like, gill-openings two pairs; branchial arches four; maxillary bones present, both jaws bear teeth; two pairs of very small and functionless limbs with two or three digits. Occurs in swamps and muddy waters of North America.

2. *Amblystoma* (family *Ambystomidae*). With a series of palatal teeth in a nearly straight, transverse line; toes five; show phenomenon of paedogenesis, i.e., larva becomes sexually mature and reproduces. Rest as in *Amphiuma*. North and Central America.

Axolotl Larva (Fig. 5.53). In the two genera, *Amblystoma* and *Triton* the larva have the power of developing sexual organs and reproducing Paedogenesis, Neoteny). The axolotl larva of *Amblystoma* has a tail-fin, three pairs of external gills and four pairs of gill-openings. It breeds several times a year, and is found in a state of nature in various

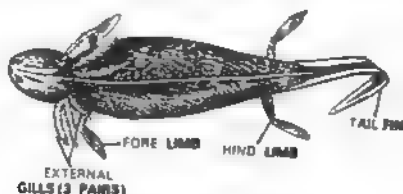


Fig. 5.53. Axolotl larva.

parts of Mexico and the United States of America. The causes of this phenomenon appear to be the abundance of food and other favourable conditions of life.

The axolotl has been known for centuries now. Its history dates back to the 16th century when, it is said, the Spanish settlers used it as food. Wagler in 1830 for the first time named it *Siredon pisciformis* thinking that it was related to the perennibranchiate *Siren*. The perennibranchiate Amphibia (suborder *Meantes*) are those amphibia that retain gills permanently and retain the form of the larva throughout life. They do not undergo metamorphosis. The popular name 'axolotl' has been derived from the Aztec Indian words 'atl' meaning water and 'xolotl' meaning servant (axolotl servant of the water).

In 1865 some individuals were brought to France to the *Jardi, des Plantes* in Paris. There they started to breed and curiously enough their young went through all the changes characteristic of metamorphosis. They lost their gills and fin, shed their larval skin, emerged as animals different from larvae. The axolotl were finally identified as sexually mature larvae of *Ambystoma*. Animals which breed as juveniles or larvae are described as neotenus (Gr. *neos*, youth + *tenio*, to extend) and the axolotl was one of the earliest examples of Neoteny to be discovered. Several other neotenus animals have since been observed, and a new interest in them was aroused because it was realised that by means of Neoteny quite large steps in evolution might occur. If a larva becomes sexually mature and able to produce offspring like itself a race of neotenus individuals quite different from the original adults may evolve. Since the species of *Ambystoma*, whose larva axolotl was not known as such, it was called *Ambystoma mexicanum*. In 1939 Habart M. Smith pointed out that it should be called by the first



Fig. 5.54. Tiger salamander, *Ambystoma tigrinum*.

name as such it was called *Siredon mexicanum*. Brunst (1955) calls the metamorphosed axolotl *Ambystoma* and the neotenuous form *Siredon* using the specific name *mexicanum* for both of them.

3 *Triton cristatus* (family Salamandridae). The European crested newt. Aquatic newt with eyelids and laterally compressed and serrated tail; fingers four and toes five; larvae attain sexual maturity if prevented from metamorphosing. Great Britain and Europe

4. *Salamandra*. European "fire" salamander. Tail sub-cylindrical and retained throughout life. It is black with yellow spots, 6" long. Adults terrestrial, eggs retained and develop for 10 months in female, then released in water.

Suborder 3. Mesantes. The Urodela with slender elongate body, without eyelids or limits. Gills persistent. Jaws are provided with horny covering. Fertilisation probably takes place outside. They are strictly aquatic. South-east United States and America.

Siren lacertina or "mud-eel" is found in Virginia and Indiana to Florida and Texas in muddy ditches and ponds. It grows to 30 inches. Body is eel-like, gill-openings are three; premaxillaries and mandibles toothless, but with horny beaks. Fore-limbs weak and with four fingers.

Subclass and order 2. Anura (Salientia). The frogs and toads form a natural group of Amphibia characterised by short, tail-less bodies and long legs. All are scaleless with a large depressed head and a wide mouth. Eye-lids are well developed and a nictitating membrane is present. Tympanic membrane large and sometimes concealed beneath the skin. The vertebral column is remarkably short, and is without ribs and tail. Nasal openings are situated on the extremity of the snout. Hind-limbs are much larger than fore-limbs. Posterior part of the tongue is completely free and can be protruded as a prehensile organ. The order is divided into five suborders and several families. Here only a few examples are given.

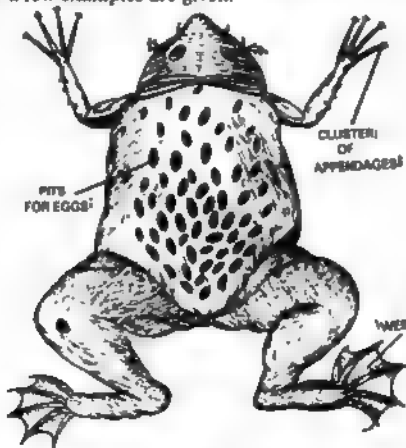


Fig. 5.55. *Pipa americana*

Bufo (family Bufonidae). Toads. Teeth absent; tympanum usually distinct; fingers free; toes more or less webbed, tips dilated into small discs, skin covered with ugly warts.

Hyla (family Hylidae). Tree-frogs. Upper jaw with teeth, terminal phalanges claw-shaped and swollen at the base and carry adhesive cushions with which these animals climb trees, tympanic membranes large. Excepting *H. arborea* and two other species found in North-India and South China, the rest are exclusively American or Australian.

Pipa americana or **Pipa pipa** (family Pipidae). The skin on the back of the female soft and spongy during the breeding season and the eggs are placed on it by the males. Each egg sinks into a little pouch of the skin covered by a gelatinous film. Embryos do not pass through any larval stage, but are hatched in the adult form.

In addition to the above families the order contains three more families, viz., Engystomatidae, Pelopodidae and Iscoglossidae.

Subclass and order 4. Gymnophiona. Vermiform amphibia without limbs or limb-girdles, tail very small or absent, with numerous small scales embedded in the skin arranged in transverse rows, eyes small, functionless and covered by skin; tympanum and tympanic cavity absent. Burrow in the surface soil in damp places near streams. Central and South America, Equatorial Africa, India and the Malaya Archipelago.

Example: *Ichthyophis glutinosa*.

6. Class Reptilia

The Class Reptilia (L. rept, creeping) includes the craniates completely adapted to life on dry land both as adult and during embryonic development. The skin is dry and is covered with horny epidermal scales to prevent loss of moisture from the body and facilitate living on rough surfaces. Two pairs of pentadactyle limbs with horny claws are used for running, crawling or climbing. Aquatic forms (turtles) have paddle-like limbs, which may be reduced in some lizards with monocondylic skull. Heart is imperfectly four-chambered (perfectly 4 chambered in crocodiles) with one pair of aortic arches. They respire by lung except some aquatic turtles that have cloacal respiration. Body temperature is variable (poikilothermous) according to environment. Fertilization is internal. Eggs are large with much yolk in leathery or limy shells. The eggs are usually laid (oviparous), but retained in female for development by some lizards and snakes. Embryonic membranes (amnion, chorion, yolk-sac and allantois) are present during development. Young resemble adults, there being no metamorphosis.

ORIGIN OF REPTILES

The amphibians retained a conservative mode of development and consequent association with water, but the reptile evolved a type of egg which can be laid on land getting complete emancipation from the water by giving up the aquatic stage in life-history.

The living reptiles include only a few groups mainly turtle, crocodiles, lizards and snakes, vastly overshadowed in importance today by the birds and mammals descended from them. It is now certain that the reptiles have evolved from Palaeozoic amphibians, but there is no agreement with regard to the 'Proreptilia' or 'Proto-reptilia'. The extinct progenitors of the reptiles are cotylosaurs, which have been referred to as the "stem-reptiles". The first traces of these are found in the Carboniferous, in the deposits formed in the great coal swamp when the amphibians were at the peak of their development.

According to the most accepted view *Seymouria* (of Pre-carboniferous) is the ideal stem-reptile. It forms a good structural connecting link between (labyrinthodont) amphibians and primitive reptiles. It possesses characters both of amphibians and reptiles. Some authors consider it to be a reptile-like amphibian while there are others who call it amphibian-like reptile. That means the *Seymouria* was an amphibian which was almost a reptile or it was a reptile which has just ceased to be amphibian. This controversy emphasized that this animal connects the two groups of amphibians and reptiles.

Eryops was once supposed to be a 'pro-reptilian' type (Gadow, 1909), but it seems to be definitely an amphibian in general structure and in both its exo- and endoskeletal patterns. Watson (1926) showed *Diplovertebron* to be an exact transitional form between such primitive amphibia as *Palaeogyrinus*, on the one hand, and *Seymouria*, on the other.

Contemporary to *Seymouria* were *Diadectes* and *Captorhinomorphs* which although reptiles, by 'definition', of a very primitive grade had their own marked specialization. Already in them *Diadectes* was on the road to chelonians while *Captorhinomorph* to typical reptiles and mammal-like reptiles; *Diadectes* was somewhat more tortoise-like, and *Captorhinomorph* somewhat more lizard-like.

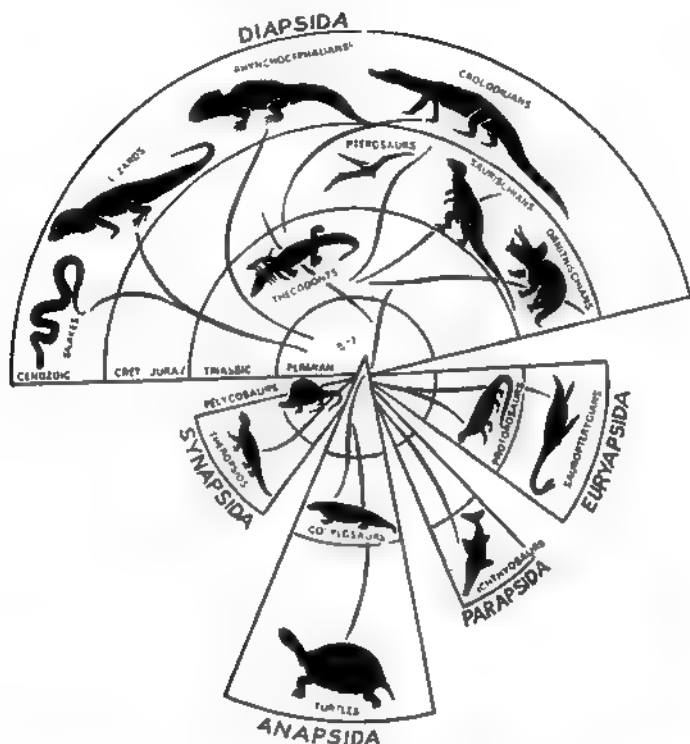


Fig. 6.1. Chart showing evolution of reptiles.

somewhat more tortoise-like, and *Captorhinomorph* somewhat more lizard-like. Because of the primitive skull features they have been put under Cotylosauria or 'stem-reptiles'. *Limnoscelis* from Lower Permian seems to be, in its general organisation, the first undoubted reptile (Romer 1947) and probably may be taken to be, or nearer to, the 'Protoreptile'.

Cotylosaurian radiation could persist hardly up to Permian and by Triassic they were already extinct. Of these varied cotylosaurians only the least specialized early forms could evolve and multiply giving place to the well-known Mesozoic reptilian radiation, which included the enormous varied members—the terrestrial, quadrupedal and bipedal flying giants, and the marine paddlers. Mesozoic was the age of Reptile, today only a little of that great population is represented, majority of them having died out, of which lizards, snakes and crocodiles and chelonians are too specialized and some time degenerate also, while *Sphenodon*, 'the living fossil' claims to retain the primitive features of Triassic time with least change.

Thus the earliest large land herbivores were probably the 'pariasaurs'; these were later replaced by other reptilian types including sauropods (in so far as these were terrestrial) and various types of Ornithischia, perhaps by the nodosaurs in the more watery habitats and the stegosaurs, and *Ankylosaurus*, *Ceratopsia* on drier ground. Finally all these gave place to the earliest mammalian herbivores, which were in turn replaced by others.

Throughout early tetrapod evolution there is a tendency to return to the water, perhaps under some pressure of competition from descendants on land. This is marked among reptiles, where besides the chelonians and ichthyosaurs and plesiosaurs there are the phytosaurs and crocodiles, and among Squamata the mosasaurs and tylosaurs, not to mention the latter aquatic lizards and snakes.

The large size of many reptiles have been one of their most striking features, but it is of course not true to say that there is a strong tendency for size to increase in all reptile groups. While many have become enormous, others, such as lizards, have produced probably as great a biomass spread over huge numbers of small individuals. It is not certain what advantage is gained by a reptile from large size, since it is not warm-blooded. Up to a certain stage, size is a protection, but it involves the dangers of those who place all the eggs in one basket, incidentally, the actual eggs of these large animals must have provided formidable physical problems for their support.

Parallel evolution in several lines, descended from a single stock, is as common among reptiles as other groups of vertebrates. Thus the bipedal habit, with hind legs longer than the front, has been adopted independently by a number of diapsids, again, elongated jaws are found among fish-eaters, whether ichthyosaurs, plesiosaurs, phytosaurs, crocodiles, or mosasaurs.

Many of the conclusions that appeared from study of vertebrate evolution in water also apply to the forms which have come on land. The fossil record leaves no doubt that almost all the populations have changed very markedly. No form of reptile, alive today, is closely similar to any found in the Permian or Triassic periods. *Sphenodon* has shown relatively less change than most other forms and it is significant that it is found in an isolated island region.

Quadrupedality, so characteristic of Synapsida, the mammal-like reptiles, led to emergence of Mammals. Bipedalism experimented by way of Diapsida led to evolution of birds. Although it is difficult to see in all this, any persistent tendency except to change, yet the very fact that each type is so rapidly replaced, suggests that descendants, in some way more efficient, are continually appearing. In the case of the reptiles the more interesting of these are the birds and mammals. Meanwhile, it may be emphasised once again that the reptiles surviving today, although not of large size, are obviously better suited for life than their mesozoic ancestors and exist in considerable numbers alongside and even in competition with the birds and the mammals.

Modern reptiles cover only four out of three dozen or more main lines that have existed in the past. Of these the most successful ones are the lizards and the snakes (Squamata). The crocodiles (Crocodylia) come next but they are an older offshoot from the same stock from which modern birds have originated. *Sphenodon*, the tuatara lizard of New Zealand, is the third group and is a relic of the past carrying many primitive features. The fourth group comprises tortoises and turtles (Chelonina) and has retained the organization of still earlier times. The four groups are the only survivors of the reptiles that flourished throughout the Mesozoic culminating in the giant Dinosaurs of the Jurassic and Cretaceous. Two types of reptiles have been described below: *Uromastix* a common lizard and *Kachuga* a chelonian.

TYPE UROMASTIX

Lizards. The lizards have been defined as reptiles with movable quadrate bones, the right and left halves of the mandibles united by suture, a transverse anal opening, paired copulatory organs, a cloacal bladder and with the anterior end of the brain case never completely closed. The body in the majority is covered with horny epidermal scales, usually possessing four well-developed (sometimes degenerated) limbs, and have eyes with movable eyelids. Majority of lizards are terrestrial. Some (chameleons and the flying-lizard, *Draco*) are entirely arboreal and some (*Dibamus*) are almost entirely subterranean. The terrestrial forms are associated with a depressed form of body, arboreal with compressed forms and subterranean with an elongated and cylindrical one. Here *Uromastix* has been described as a type of the group. The description, however, can be safely used for the study of other lizards such as the

ordinary wall-lizard or the monitor-lizard (*Varanus*.)

Uromastix or the spinny-tailed lizard, inhabits sandy tracts where the vegetation is scanty and feeds upon grass, flowers and fruits. Each one lives in its own burrow, four to eight feet deep. The lizard is widely distributed over the area in which it occurs and is common in many places. In the northern part of its range, at any rate, it does not leave the burrows until the sun is up, and after feeding returns to the burrow during the heat of the day. At sunset or earlier, if the temperature is low, it retires for the night, carefully closing the entrance to the burrow. In the winter month it hibernates. In the spring they pair and separate. The eggs are large measuring 20 to 30 mm. in size. Each female is reported to lay as many as fifteen eggs.

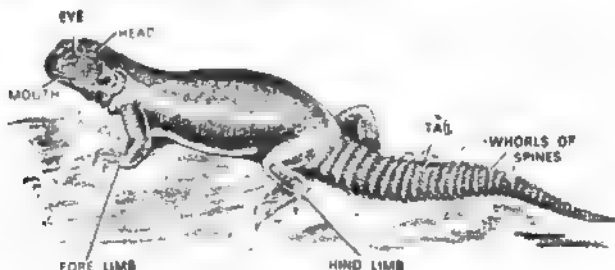


Fig. 6.2, *Uromastix hardwickii*.

Uromastix is of a placid and gentle disposition and is tamed soon in captivity. In its movement it is slow. When disturbed it tries to frighten away the disturber by lifting its head in a peculiar way opening its mouth at the same time. Some tribes in the hilly regions of Rajasthan take it as a food and its meat is said to be excellent, sweet like chicken. The tail is considered to be a delicacy. They catch it by digging out the burrow or by filling it with water thus forcing the lizard to wriggle out.

An interesting account has been given by Purves about the method used by *Uromastix* to protect itself from snakes. On hearing the rattle of a snake it enters into the burrow, keeping three or four inches of its tail outside the mouth and shaking it violently. The snake attacks it but is hurt badly by the horny spines on the sides of the tail. This finally drives the snake away. On the other hand, if the snake can get into the hole before the lizard can get its tail outside it becomes defenceless and is caught by the head by the snake and eaten. The fat of the body is boiled down and the resulting oil is used as an embrocation and also as a cure for impotency.

Uromastix hardwickii occurs in north-western India as far east as Uttar Pradesh. Specimens from Sind and Kathiawar differ slightly from those of other regions, but the variation is not sufficient to warrant racial distinction.

EXTERNAL FEATURES

The body of *Uromastix* is depressed without crest, and is covered by scales (Fig. 6.2). Upper head scales are unequal smooth or obtusely keeled, large on the snout small over the outer part of the upper eyelids. The scales on the cheeks are oval, 12 to 14 upper labials, more or less, denticulated on their free margins. Dorsal scales are very small, subequal, mostly smooth with (or without) scattered larger ones upon the back; these are sometimes numerous. The enlarged dorsal scales, arranged in cross series, are always present. The ventrals are subquadrangular in shape as large or larger than the largest dorsals. Gular scales are rounded much smaller than the ventrals. Skin of the neck and sides of the body are very loose with a more or less distinct transverse fold across the throat. The depressed tail is covered with whorls of spinose scales. In colour it is yellow brown above, uniform or with dark spots or vermiculations, and whitish

below. There is a large blackish spot on the front of each thigh. The throat is often furnished with black spots. They attain a larger size reaching a total length of 350 mm.

The mouth is a wide slit-like aperture running along the anterior border of the head. Situated above the anterior extremity of the head, there are two large apertures, the nostrils. The eyes are large, at the sides of the head, provided with two, the upper and the lower, movable and opaque eyelids. A transparent nictitating membrane is also present which lies folded at the anterior angle of the orbit when withdrawn. In *Gekko* the eyelids are fused forming a transparent covering as in snakes. A circular, brownish patch of skin, the tympanic membrane, is deeply sunk below the general surface of the skin on each side behind the eye. Anterior border of the ear opening is feebly denticulate.

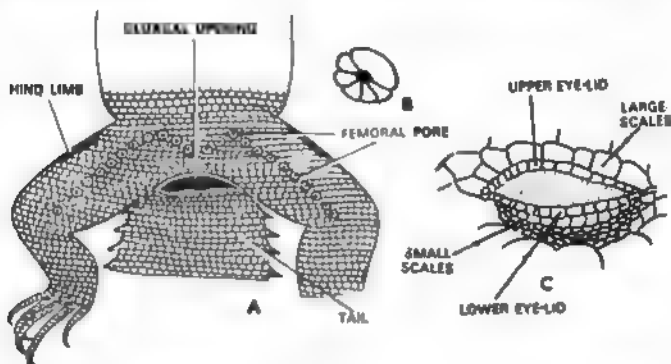


Fig. 6.3. A, ventral view of the posterior part of the body of *Uromastix* showing opening of the cloaca and the femoral pores; B, one femoral pore surrounded by scales of which one is quite large; C, scales surrounding the eye.

The trunk is elongated, flatter ventrally and convex dorsally. It is supported by two pairs of strong, short pentadactyle limbs. The fore-limbs arise from the trunk just behind the neck. Each consists of the upper-arm (brachium), the fore-arm (antibrachium), and the hand having five clawed digits, the first digit (pollex) is the smallest. The hind-limbs are situated towards the end of the trunk more towards the ventral side. Each has a thigh (femur), shank (crus) and a foot (pes) having five digits with horny claws, the first or hallux is the smallest. On the other under side of the manus and pes in *Gekko*, leaf-like adhesive pads are present. The surface of the pads on each is divided by a series of transverse plates. They help them climb smooth vertical surfaces. In *Uromastix* and *Varanus* the limbs are used for digging. A slit-like transverse aperture of the tail, the cloacal aperture, occurs on the ventral surface. On the under surface of the thigh occur the preanal and femoral pores. There are twelve to eighteen preano-femoral pores on each side. These are openings of simple tubular ectodermal invaginations. The femoral pores are arranged in a single row along the under surface of thigh. The preanal pores may form an angle, the apex forwards, or be arranged in a cluster. Each preanal and femoral pore is surrounded by a complete ring of minute scales of which one is larger in *Uromastix* (Fig. 6.3 B). The tail is dorso-ventrally compressed structure, thick in front, oval in section, and gradually tapering to a narrow posterior extremity. Dorsally the tail is covered (Fig. 6.2) with cross series of enlarged, squarish, juxtaposed, spinose scales. The scales are the largest on the sides. These rows of spines are separated from one another by four to six rows of keeled scales. The lower surface of the tail is covered with squarish scales about as large as the ventrals. Some lizards break off their tails very easily to keep the attention of their enemies engaged to it while they escape. The tails regenerate later on.



Fig. 6.4. Photograph showing scales of dorsal side. A, scales under lower power; B, under high power.

Skin. The skin is normally covered with scales, the horny epidermal coating of which is periodically shed. In the majority of lizards it comes off in flakes, but in those which have a much elongated body it may be shed in one piece. The scales usually have a free posterior border and, more or less, overlap one another. In geckoes the scales are replaced by tubercles or granules. In some lizards osteoderms occur. These are ossifications of cutis in the form of small bony plates. Osteoderms are found in *Varanus salvator* but not in other Indian species. In *Uromastix* also they are absent. The dorsal scales of *Uromastix* are uniform in size and rounded or oval in shape. Those on the ventral side are quadrangular (Fig. 6.5).

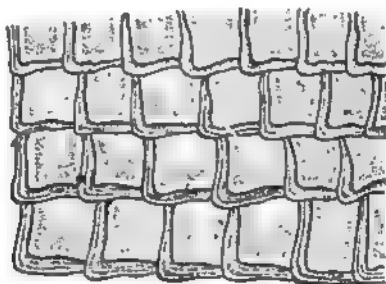


Fig. 6.5. Scales on the ventral side of the body.

ENDOSKELETON

The structure of the endoskeleton of *Uromastix* has not been worked out in detail. Usually the skeleton of *Varanus* is studied in its place, the same is described here.

The vertebral column of *Varanus* consists of a large number of vertebrae usually, divided into cervical, thoracic (thoracolumbar), sacral and caudal regions. A typical cervical (Fig. 6.6) consists of a stout centrum which is hollow in front and convex behind, i.e., procœlous. The neural arch bears a prominent crest-like neural spine. Anteriorly it bears articular facets, the *prezygapophyses*, that are directed upwards, and posteriorly other set of articular facets, the *postzygapophyses*, that are directed

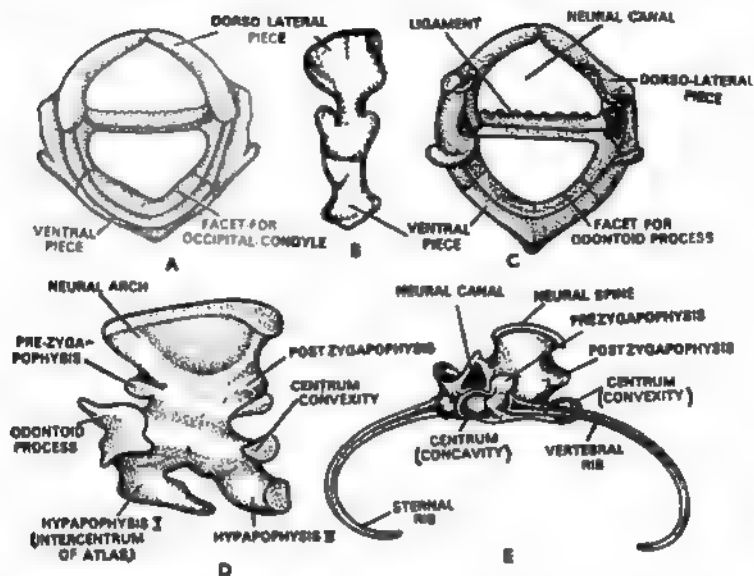


Fig. 6.6. Vertebrae of *Varanus*. A, anterior view of atlas; B, side view of the same; C, side view of axis; D, anterior view of thoracic vertebra.

downwards. The centrum bears a backwardly directed posterior process, the hypapophysis, on the ventral surface. All the vertebrae behind the third have articular surface for the cervical ribs. The first cervical vertebra or atlas is modified to articulate with the skull. It is ring-like having no distinct centrum. In fact the ring is made up of three bony pieces, one ventral occupying the place of the centrum and two dorsolateral arching over the ventral. The latter two do not meet in middle though they appear so, as the space in between them is filled by membrane. A transverse ligamentous band is seen dividing the ring of the atlas into two. Ventrally, on its anterior face, is found an articular facet for the occipital condyle. The second cervical or axis (Fig. 6.6) vertebra is just like a typical vertebra in structure, but it is slightly larger and bears a hook-like process intercentrum of the first vertebra, on the ventral surface of the centrum towards its anterior end. The pointed tip of the process is directed towards the hypophysis. The neural spine is a larger plate-like structure. The prezygapophyses are represented by mere notches whereas the postzygapophyses are as usual. The centrum bears a broad odontoid process on its anterior face. The thoracolumbar (Fig. 6.6) vertebrae that follow the cervical are like the typical cervical, as described above, but for the fact that they are somewhat larger and that each bears prominent articular facets, the capitular facet, at the junctions of the centrum and the neural arch, for the articulation of the ribs. The first new thoraco-lumbar vertebrae also bear hypophyses ventrally which go on dwindling in size and finally disappear in subsequent vertebrae. The sacral (Fig. 6.5) vertebrae are two in number and articulate with the ilia, of the pelvic girdle. They are, therefore, very stout. The centrum in each case, is stout and short, and bears strong expanded transverse processes. The tips of the transverse processes of the anterior vertebra are deeply notched to provide articulation space for the ilia. The caudal vertebrae (Fig. 6.7 C) are numerous and become gradually smaller towards the posterior side, so much so, that at the end of the tail the whole vertebra is just a bony rod. The anterior caudal vertebrae have relatively

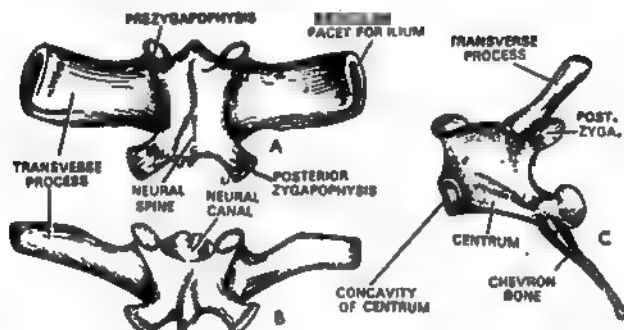


Fig. 6.7. Dorsal view of the sacral vertebrae. A, first sacral; B, second sacral; C, side view of the same.

longer central, slender transverse processes and longer neural spines. These vertebrae have Y-shaped chevron bones attached to the ventral surfaces of the centra. Two upper limbs of Y-articulate with the centrum, thus enclosing the neural canal.

Ribs and Sternum. The ribs (Fig. 6.6) are slender curved rods. They are single-headed and are attached to the vertebrae between the centrum and neural arch. Excepting the first three vertebrae, all precaudal vertebrae bear ribs. The cervical ribs are short rods not connected with the sternum. The thoracic ribs are relatively larger and are connected with the sternum by cartilaginous sternal ribs in the first three thoracic vertebrae. The fourth carries a little cartilaginous rod attached to its free end representing the dwindling sternal rib. In other vertebrae the ribs are short and free ventrally (not connected with the sternum).

The **sternum** (Fig. 6.8) consists of rhomboidal plate of cartilage from the posterior end of which articulate two sternal ribs. From its posterolateral edges articulate two

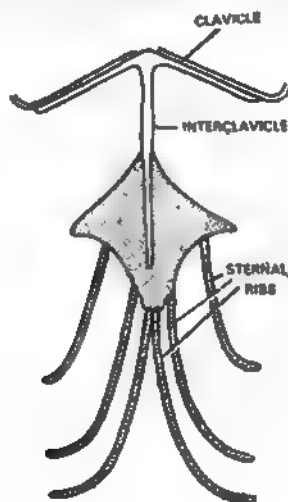


Fig. 6.8. Sternum of *Varanus*.

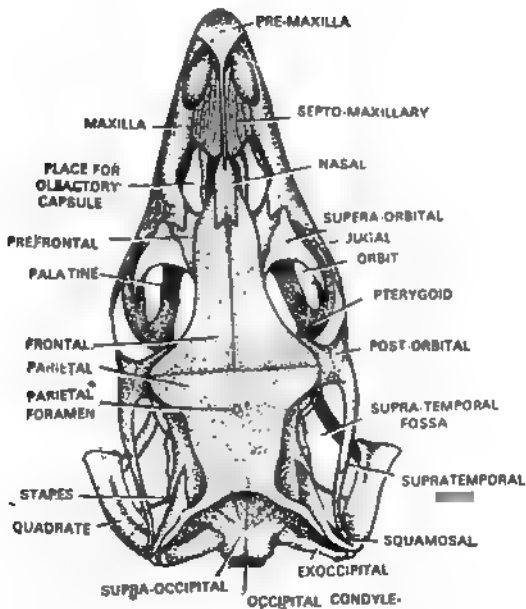
sternal ribs on each side. Anteriorly the apex is drawn out to a long narrow rod of cartilage, the *interclavicle*, which ends forming a T-shaped structure. The vertical limb of T continues on the ventral surface of the sternum; on the small anterior arms of T rest the two clavicles of either side. The bones of the pectoral girdle articulate with the antero-lateral borders of the rhomboidal plate.

Skull. The skeleton of the head, like that of the frog, consists of the cranium proper, olfactory and auditory capsules and the visceral skeleton, which, including the jaws, hyoid bone and auditory ossicles, is so closely associated with other parts that it is convenient to describe all the parts under 'skull'. The cranium proper forms the posterior part of the skull and lodges the brain. In *Varanus*, as in other lizards, some important bones of the cranium such as the alisphenoids, orbitosphenoids and presphenoids are missing. In birds and mammals these bones form a major part of the cranium ventrally. In *Varanus* this part of the brain-box is formed by membranes. The occipital segment forms the posteriormost part of the brain-case around the foramen magnum. It consists of four bones, which are fused inseparably. Of these *basal-occipital* forms the base, the *exoccipital* the sides, and the *supraoccipital* forms the roof. The *basal-occipital* carries the *occipital condyle* mainly formed by it (*basal-occipital*). The *parietal* segment consists of a broad *basal-sphenoid* with two prominent processes at its anterior sides forming the base, and the *parietals* forming the roof. The two *parietals* are fused completely in the adult, even a suture is not visible. The *parietals* are narrow posteriorly and broad anteriorly. A *parietal foramen* is found on the parietal situated a little anterior to the suture of the parietal with the frontals on the mid-dorsal line. The sides of the parietal segment are not covered by bones, as in higher animals, the alisphenoids are absent and membranous tissue that takes their place is removed while cleaning the skull.

A careful examination reveals that the *parietals* are not joined with the *supraoccipital* by suture but there is a distinct gap filled up with fibrous tissues, that is removed during cleaning. The *fronto-parietal* part of the skull is slightly movable upon the *occipito-sphenoidal* part. The frontal segment is incomplete. It is without a base as the *presphenoid* is absent, and without sides as the *orbitosphenoids* are also absent. These are replaced by membranous tissues. The roof, however, is formed by the paired *frontals* that are suturally fused in the middle line. Posteriorly the *frontals* are separated from the *parietals* by a distinct coronal suture. The olfactory capsule is dorsally covered by the *nasals* and floored by the *vomers*. The *nasals* are flat triangular bones fused in the middle. The rod-shaped *vomers* are two, separated posteriorly but fused with each other anteriorly. They form the inner margin of the posterior, *nares*. The auditory capsule (Fig. 6.12) usually consists of the *opisthotic*, *epiotic* and *prootic*, of which, in this animal, the *epiotic* is fused with the *supraoccipital*, the *opisthotic* is fused with the *ex-occipitals* and only *prootic* remains separate.

The *supraoccipital* consists of *parotic process*, the *squamosal* and the *quadrate*. The *parotic process* is formed by the prolongation of *exoccipitals* and *prootic*. Each is a horizontal process directed outwards, slightly backwards, on either side of the foramen magnum, and articulates with the *squamosal* and the *quadrate*. The *squamosal* (Fig. 6.9) is a short bony rod bending forwards and upwards, attached to the *parotic process* posteriorly. Anteriorly it extends forwards to the *postfrontal* (except in geckos) forming the *supra-temporal arcade*. The *quadrate* (Fig. 6.10) is rod-like bone attached to the anterior aspect of the *parotic process* directed forward and downwards articulating with the *pterygoid*.

The *temporal region* is distinctively developed in the reptiles. The *posterior temporal fossa* (Fig. 6.11) is a cavity guarded ventrally by the *parotic* and dorsally by *parieto-squamosal* or *posterior temporal arcade*. The *parietal* sends out a process posteriorly which fuses with the *squamosal* forming the *parieto-squamosal*. The *supratemporal fossa* is the cavity between the *supra-temporal arcade* (formed by the union of the *squamosal* and the *post-frontal*) and the *parietals*. The *lateral temporal fossa* (Fig. 6.12) is bridged over by the *supra-temporal* and its posterior margin is formed by the *quadrate*. Ventrally it is open as the *quadrate-jugal* is absent and no *infra-temporal arcade* is formed, and anteriorly, also the fossa is not closed as the *jugal*

Fig. 6.9. Dorsal view of the skull of *Varanus*

is not joined with the post-frontal. Thus, the orbit and the fossa communicate.

The orbits (Fig. 6.12) are large and closely approximated being separated by only a thin vertical interorbital septum. Dorsally it is roofed over by the frontals and anteriorly it is bound by a small bone *prefrontal* and another perforated bone, the *lacrimal*. Posteriorly the orbit is incompletely bound by the post-frontal (dorsally) and jugal (from ventral side.) Another triangular bone, *supra-orbital* overhangs the orbit. Its flat base is attached to the anterior angle of the orbit formed by the prefrontals and the lacrimal while the pointed free end is directed towards the postfrontal.

The bones of the *maxillo-palatine apparatus* include the pre-maxillae, septomaxillary and maxillae. The premaxillae (Fig. 6.12) are fused in the middle forming the anterior extremity of the snout. The median bone, thus formed, bears six to eight small teeth. The septomaxillary process (Fig. 6.12) is a small bone on each side just above the vomer in the anterior part of the nasal region. The maxillae (Fig. 6.9, 6.12) are a pair of irregular bones forming a large part of skeleton of the upper jaw. Its body is called alveolar portion as it bears teeth. The palatine process is not well developed in this case, thus, leaving space between the maxilla and a palatine. The maxilla bears conical teeth ankylosed to the bone, by their sides just inside the edges of the jaw (pleurodont). The palatines (Fig. 6.10) are irregular bones and pass backwards from the vomers and the maxillaries to the pterygoids. The pterygoids (Fig. 6.10) are again irregular bones; which, diverging from one another, extend backward to the quadrate articulating in the way with the lateral process of the basi-sphenoid. Extending between the pterygoids (in the next page) and the parietal (above) of each side there is a rod-shaped bone led the *epipterygoid* which is also called *columella cranii* (to avoid confusion with the *columella auris* it is better to call it *epipterygoid*.) The *transpalatine* (Fig. 6.10) is a small bone passing from the palatine and pterygoid to meet at the junction of maxilla and jugal.

The lower jaw (Fig. 6.13) consists of two rami each up of 6 bones, the dentary,

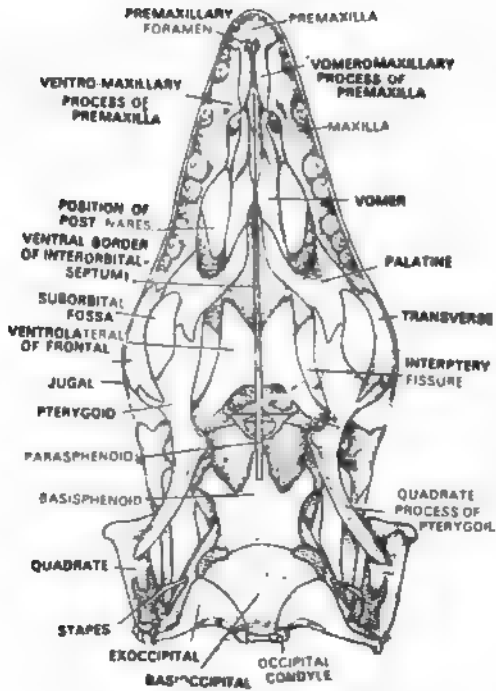


Fig. 6.10. Ventral view of the skull of *Varanus*.

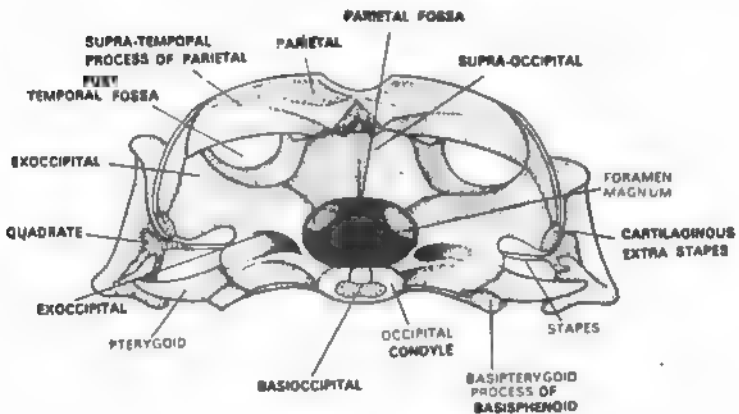
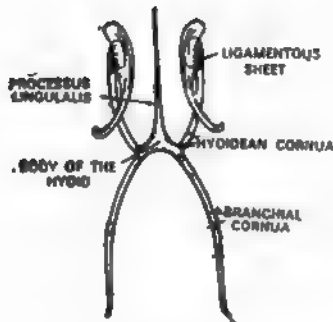
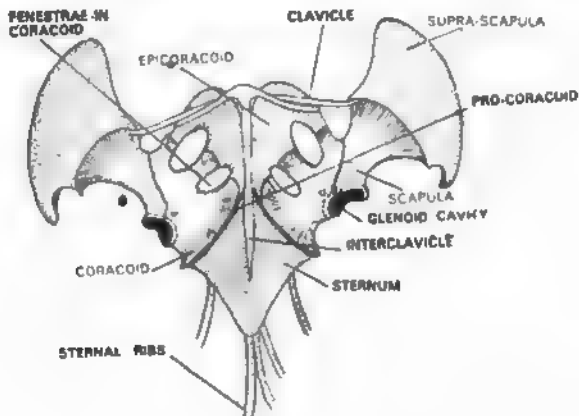


Fig. 6.11. Posterior view of the skull of *Varanus*.

Fig. 6.14. Hyoid apparatus of *Varanus*.

portion, the coracoid proper. The epicoracoid, an irregular-shaped cartilage starting from the proximal end of the coracoid, runs along the inter-clavicle up to its end, whence it bends back and runs to the mesoscapula. Before running back it also gives a process to the mesocoracoid. Thus, the whole of the epicoracoid appears fenestrated. The interclavicle or episternum is a cross-shaped investing bone, the stem of which is longitudinal and is in the posterior portion of its extent, closely applied to the ventral surface of the anterior part of the sternum, while the cross-piece is situated a little in front of the scapula. The clavicles are flat curved bones articulating with one another in the middle line and also with the outer end of the interclavicle.

The fore-limbs show the usual pattern of the pentadactyle limb. The arm (Fig. 6.16) consists of the humerus, both ends of which are greatly expanded. The head lies at the proximal end and the distal end has pulley-like articular surface, the trochlea, that articulates with the radius and ulna. A prominent crest-like deltoid ridge is also present. The forearm consists of two bones radius and ulna, of which the radius is slender consisting of a shaft and two epiphyses. Distally it has a concave articular facet for the carpus. The ulna is stouter, its proximal end is produced into an upwardly directed olecranon process. While the distal end bears a convex articular surface for

Fig. 6.15. Pectoral girdle of *Varanus*.

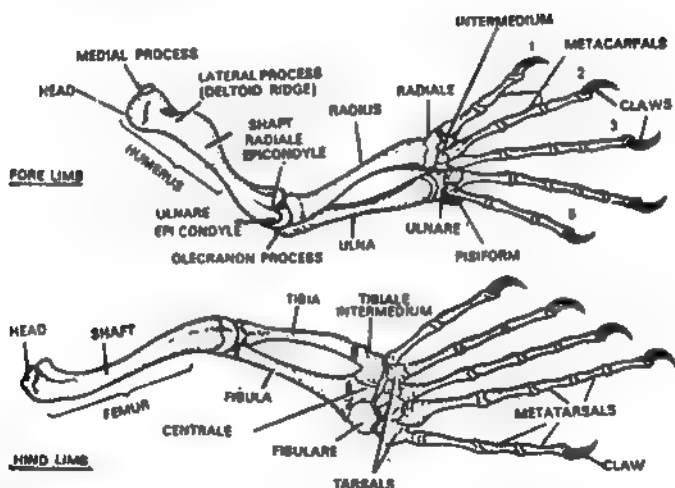


Fig. 6.16. A, Dorsal view of the right hind-limb of *Varanus kribia*. B, Dorsal view of the right fore-limb of *Varanus kribia*.

the carpus. The carpus consists of ten polyhedral carpal bones arranged in three rows. The proximal row consisting of three, (the radiale, ulnare, and intermedium), the central row of one (centrale) and the distal row of five small pieces. Besides these, the pisiform is attached to the distal epiphysis of the ulna on its post-axial side. The digits are five each consisting of a metacarpal bone and varying number of phalanges. The first digit (pollex) has two phalanges, the second three, the third four, the fourth five and the fifth has three only.

The pelvic girdle (Fig. 6.17) consists of the ilia, pubes and ischia which form two triradiate bones, the ossa innominate. The ilium is a compressed rod passing upwards and backwards to articulate with the sacral vertebrae. The pubis, on each side, passes

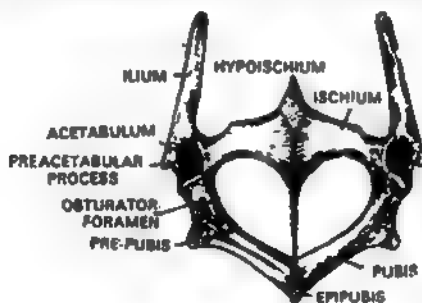


Fig. 6.17. Pelvic girdle of *Varanus*.

to meet its fellow in the middle line at the pubic symphysis. Between the anterior ends of the pubis, in front, is a nodule of calcified cartilage, the epipubis. On the other end, near its fusion with the ilium and ischium each pubis has an oval foramen for the

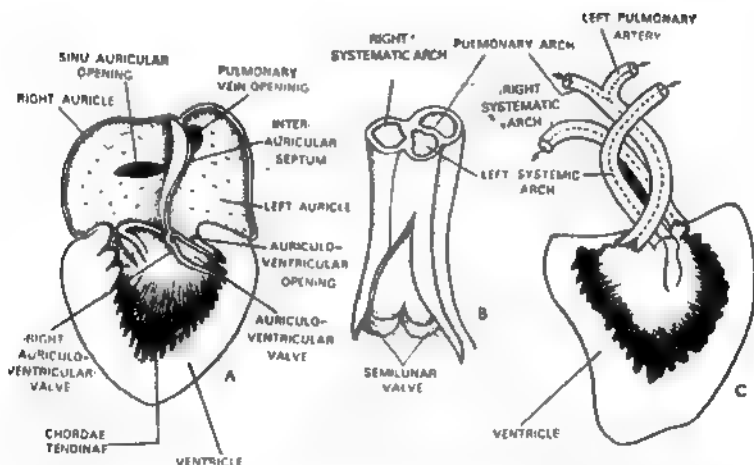


Fig. 6.21. Internal structure of the heart of *Uromastix* (after Bhatia). A, vertical section, B, the aortic arches, C, section showing course of blood from the ventricle.

behind the posterior edge of the kidney and meet in the median line (Fig. 6.23) forming a sort of loop. During their course the two efferent renal veins receive many small branches from the lumbar region. The posterior vena cava is a thin-walled vessel that passes forward to the extremity of the long descending limb of the right lobe of the liver, into which it is partly embedded. During its course it receives a vein from the vertebral column and the dorsal muscle, the vertebral vein, several small veins from the liver lobes, and two hepatic veins just before entering the sinus.

Hepatic Portal System. The hepatic portal system consists of the anterior abdominal vein bringing a part of the blood from posterior region of the body and the veins returning blood from different parts of the alimentary canal. All blood is taken to the left lobe of the liver. The main trunk of this system takes its origin posteriorly by the confluence of the following prominent veins. The oesophageal vein (Fig. 6.23) draining the oesophagus, enters to join the posterior vena cava directly into the anterior half of the left lobe of the liver. There are several gastric veins arising from the stomach. These include (a) the anterior gastric, a large vein arising near the middle of the stomach, and (b) the posterior gastric, an large vein from the posterior end of the stomach. This itself is formed by the union of a number of small branches (i) (gastric veins) from the stomach, (ii) the pyloric vein from the pylours, (iii) the pancreatic vein from the pancreas, and (iv) the duodenal vein from the duodenum. The intestinal vein formed by the union of veins from the rectum (rectal vein), colon and caecum. The anterior abdominal vein (Fig. 6.23) is formed in the midventral line by the union of two pelvic veins that are the continuations of the common iliac-veins.

Renal Portal System. The caudal (Fig. 6.23) vein starts from the tip of the tail and runs in the haemal canal of the caudal vertebrae receiving on its way several branches from the tail muscles. Behind the kidney it receives a pair of inguinal veins from the inguinal region. It then enters the hind kidney where it becomes split up into two diverging branches running forward, partially buried in the substance of the kidney. These two branches are the renal portal (afferent) veins. The renal portal vein (Fig. 6.23) of each side continues forward into the kidney on each side and ramifies, gradually diminishes in size and finally disappears. Each receives a cloacal vein from the side of the cloaca and a rectal vein from the dorsal region of the rectum and

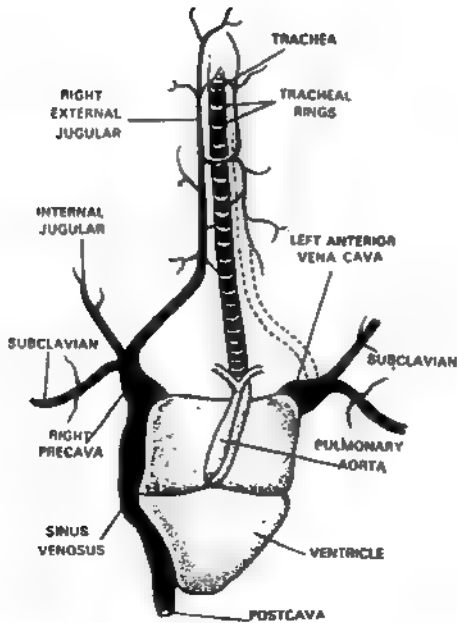


Fig. 6.22. Anterior veins of *Uromastix*.

bladder. Anteriorly each receives a fairly large vein, the **common iliac**, somewhere in the middle region of the limb of the kidney in its deep cleft at the level where the two lobes of the kidney diverge. The common iliac (Fig. 6.23) on each side is formed by the union of two branches: (a) the **external iliac** draining various muscles of the thigh and known as the **femoral** below the thigh in the distal region, and (b) **internal iliac** which is comparatively smaller and corresponds with the sciatic vein of the frog. The **pelvic veins** (Fig. 6.23) arise from the common iliac veins. After origin each passes forward laterally and then sharply turns ventrally ultimately uniting with its fellow from the opposite side in the mid-ventral line forming the **anterior abdominal vein**. During its course each pelvic receives a couple of small **parietal veins** from the posterior muscles, the **vesical vein** from the bladder, the **ischial vein** from the ischium, the **pubic vein** from pubic region, and **adipose vein** from the fat-bodies. The **anterior abdominal vein** (Fig. 6.23) is formed by the union of two pelvic veins. After the union it bends upwards, and forwards, runs over the viscera and opens into the left liver lobe. In *Uromastix* the **anterior abdominal vein** is double at places indicating a primitive feature.

There is a single thin-walled **pulmonary vein** (Fig. 6.20) of moderate size, which leaves the left lung anteriorly, and runs along the ventrolateral side of the trachea. It passes dorsally to the sinus venosus and opens into the left auricle. Actually it is formed by the union of several veins from both the lungs.

Arteries. The arterial system of *Uromastix* shows many primitive features. Two systemic and pulmonary arches arise from the ventricle. The **carotids** arise together from the right systemic by means of small common **primary carotid**. A very well-developed **ductus caroticus** connects each carotid with the systemic arch of its side. The **ductus arteriosus** is absent. The **dorsal aorta** gives off fifteen pairs of **parietals** which are segmentally arranged, and all the main branches supplying the alimentary

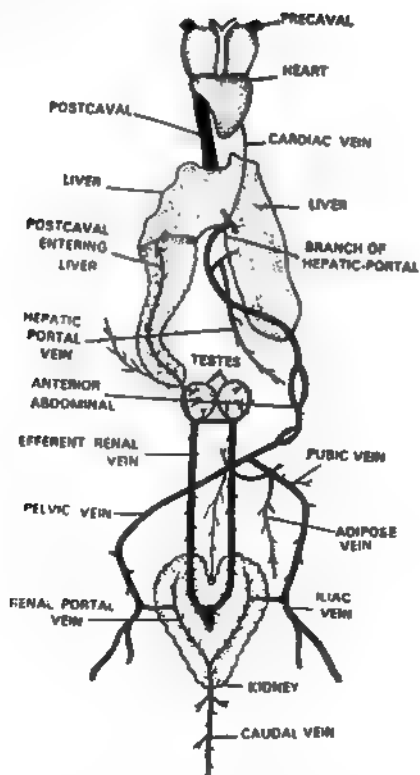


Fig. 6.23. Renal portal system of *Urodonax* (after Bhatia).

canal and the remaining visceral organs arise independently of one another.

The systemic arches (Fig. 6.24) are two, left and right. Both come off separately from the ventricle. On their anterior walls both receive the ductus caroticus from the carotid arch. They then curve round the oesophagus, become dorsal in position, and finally run back to unite with each other in the middle line to form the **dorsal aorta**. From the right systemic arch arise several important vessels, but the left systemic arch does not give rise to any. The following are the important arteries arising from the right systemic. The carotid arches (Fig. 6.24) arise from the right systemic by a small common vessel, the **carotis primaria** (primary carotid), which soon bifurcates forming the right and left common carotids. The right common carotid (Fig. 6.24) runs almost parallel to the systemic arch for a little distance and then turns forwards running along the side of the trachea. Soon, however, it divides into two, the **internal** and **external carotids**. The external carotid has a fairly wide distribution and gives arteries to the thyroid, oesophagus, trachea, floor of the buccal cavity, larynx, tongue, hyoid and its muscles, etc. The internal carotid is a fairly large branch and a little beyond its origin it receives the ductus caroticus. After that it turns forward and supplies the whole of the face, jaws and brain. The left common carotid follows almost identical course. The

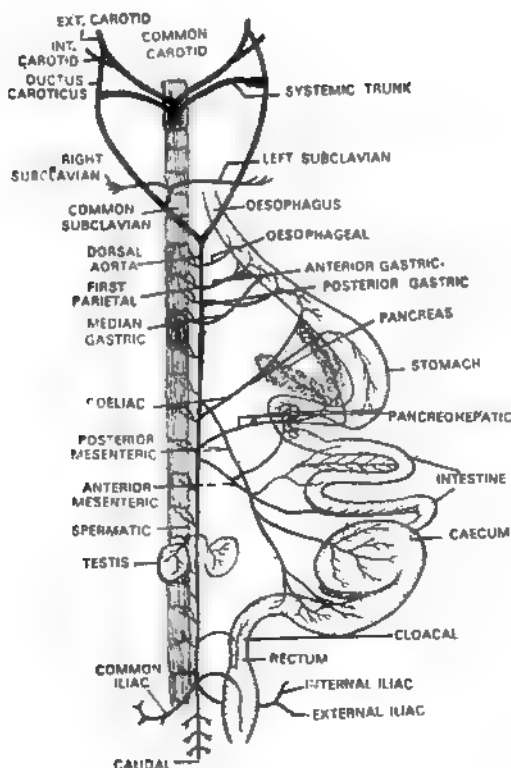


Fig. 6.25/ Arterial system of *Uromastix* (after Bhatia)

through four or five large branches. The genital arteries are a pair of blood vessels arising from the aorta supplying the genital organs. In the males they are called the **spermatic** arteries and in the female **ovarian** arteries. The **rectal** artery (Fig. 6.25) passes down along the dorsal wall of the rectum. The **cloacal** artery is the next. It also passes dorsal to the wall of the rectum and supplies the lateral wall of the cloaca and the extreme posterior end of rectum. In the region of the sacral vertebrae arise the two **common iliac** arteries (Fig. 6.25), and mainly supply the hind limbs. Each common iliac gives rise to the following branches: the **hypogastric** to the urinary bladder, the **external iliac** supplying various muscles of the thigh and running as **femoral** in the distal region; and the **internal iliac**, comparatively smaller, supplying the lower part of the leg.

Course of Circulation. The course of circulation through the heart of *Uromastix* is simple like that of the frog. All the venous blood returns to the right auricle through the sinus venosus and finally passes on into the right side of the ventricle. Owing to the spongy nature of the ventricle this blood is well retained in the right side. Meanwhile the two pulmonary veins have returned blood from the lungs to the left auricle. This is aerated blood and is contained in the left side of the ventricle. There is, however, a slight mixture of arterial and venous blood in the ventricle. With the contraction of the

arytenoid cartilages. In the gekkos (wall-lizards) the larynx is provided with vocal cords also that enable it to produce sound. The larynx leads into the trachea which lies in the mid-ventral line of the throat extending into the lungs. The wall of the trachea is provided with rings of cartilage, the **tracheal rings**, to prevent it from collapsing. On the posterior side, the trachea bifurcates to form two small tubes, the **right and left bronchi**. Each bronchus connects with a corresponding lung. The lungs are elongate fusiform sacs of orange colour lying on either side of the heart, dorsal to it, and extending posteriorly along the outer margins of the liver lobes. The walls of the lungs are thin and elastic showing large number of **alveoli**. The alveoli are ultimate subdivisions of the bronchi and it is within them that the exchange of gases takes place. Air is forced out by the return of the ribs to their resting position. The principles involved in the tissue respiration are common in all vertebrates.

NEURO-SENSORY SYSTEM

The **neuro-sensory system** of reptiles, in general, is constructed on the amphibian plan. The numerous differences in the plan of nervous system between the two groups are not apparent anatomically but reptiles, however, indicate a higher degree of nervous efficiency. One of the major differences is the absence of the **lateral line system** in reptiles. This system is peculiarly adapted to aquatic mode of life and as reptiles are purely terrestrial this system is gone. In amphibians its traces are present but not so in reptiles. The absence of this system has been fully compensated by improvements in other sensory organs. With the appearance of a horny layer some other integumentary sense organs are lost.

Brain. The brain of *Uromastix* is quite simple just like that of the frog. It consists of the usual three subdivisions, the fore-brain, mid-brain and hind-brain. The **fore-brain** consists of the cerebral hemispheres and olfactory bulb, the mid-brain consists of thalamencephalon and the hindbrain comprising the medulla oblongata. The **cerebral hemispheres** are two oval bodies somewhat narrower in front and closely applied to each other. Anteriorly each is prolonged into an **olfactory peduncle** dilated in front forming the **olfactory bulb** (Fig. 6.27). The roof (**pallium**) of each hemisphere is

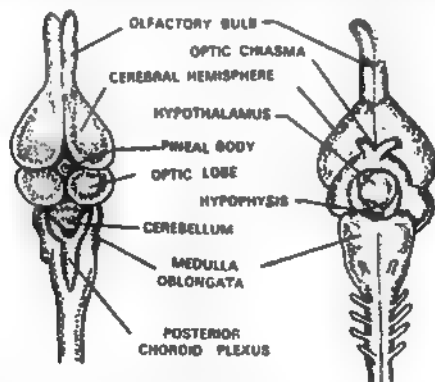


Fig. 6.27. The brain of *Uromastix*. A, dorsal view; B, ventral view.

thinner than the ventral and lateral walls, which together constitute the **corpus stratum**. The pallium however, is thicker than the corresponding part in the amphibian brain. The **diencephalon** is a small rounded area between the cerebral hemispheres and mid-brain. It is hardly visible from the dorsal side. Its lateral walls are thickened forming the **optic thalami**, but the roof is thin-walled. Behind the optic thalami passes a transverse band called the **posterior commissure**. The **pineal apparatus** arises from

the dorsal surface of the diencephalon. It consists of two parts: (a) a **parietal organ** (parietal eye) in front, and (b) a **pineal body** or **epiphysis** behind. In most lizards the parietal eye is eye-like in structure. In front of the epiphysis there is the aberrant commissure connecting the posterior parts of the cerebral hemispheres. The **infundibulum** arises from the ventral surface of the diencephalon behind this occurs the **pituitary body**. The optic chiasma lies anterior to the infundibulum. The **mid-brain** consists of a poorly developed **cerebellum** (like that of the frog) being a small anteriorly-flattened lobe overlapping the anterior portion of the **metacoele**. The **medulla oblongata** (metencephalon), the last part of the hind-brain, is broad in front, tapering behind and passes into the anterior portion of the **spinal cord**. It is slightly flexed ventrally. The spinal cord presents typical vertebrate pattern, and is lodged in the neural canal.

The ventricles of the brain are also similar to those of the frog. The **lateral ventricles** or **paracoeles** are the shallow cavities within the cerebral hemispheres, each sending a prolongation, the **rhinocoele** into the olfactory bulb anteriorly and communicating with the **diacoele** behind by a small aperture, the **foramen of Monro**. The **choroid plexus**, a vascular process passes through the foramen of Monro into each paracoele. The **hippocampi** are specially thickened areas, one on the mesial surface of each hemisphere. The two hippocampi (singular hippocampus) are connected with each other by a **hippocampal commissure** lying immediately above and behind the choroid plexus. The **diacoele** is the laterally compressed cavity of the diencephalon. Its roof is extremely thin. Its lateral walls are formed of two thickenings, the **optic thalami**. The **optocoele** is the cavity of each optic lobe. Both communicate with the **lter**, a narrow passage connecting diacoele with the metacoele. The **metacoele** (or cavity of the fourth ventricle) is the shallow cavity of the medulla oblongata. The roof of metacoele consists of special vascular tissue called the **choroid plexus** of the metacoele.

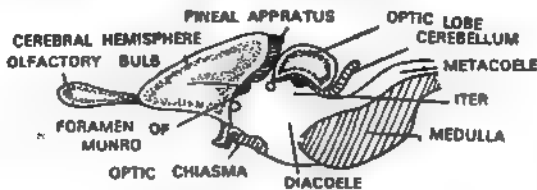


Fig. 6.28. Sagittal section of the brain of *Uromastix*.

The brain of the reptiles shows a relative increase in the size of the cerebral hemispheres and the olfactory bulbs are reduced. The increase in the size of the hemispheres indicates an enlargement of instinctive activities. The young animals have not to be taught. The animal automatically and inevitably carries out the activities which are normal and characteristic of its species. The behaviour of reptiles is certainly on a higher level than that of amphibians in general. Some reptiles can learn, remember and form new habits. They respond more quickly than amphibians. Such experiments, however, have not been performed with *Uromastix*.

The **peripheral nervous system** consists of twelve pairs of **cranial nerves** from the brain and sixteen pairs of **spinal nerves** from the spinal cord. First ten pairs of cranial nerves correspond with the ten pairs of cranial nerves of fishes and amphibians. The eleventh (accessory) and the twelfth (**hypoglossal**) arise from the extreme hind end of the brain and behind the tenth pair. The embryonic origin and the connections of these two nerves indicate that they correspond, at least in part, to certain anterior spino-occipital nerves of fishes and amphibians, but the eleventh seems to have annexed some posterior roots of the vagus. The spinal nerves arise by two roots, dorsal and ventral, as in other vertebrates.

The **autonomic system** consists of two conspicuous white trunks that extend along each side of vertebral column. Each of the autonomic trunks is connected with all the

spinal nerves on the same side of the body by a number of ganglionic enlargements. The usual sensory and motor functions are carried on by these systems. The autonomic system helps to regulate involuntary reactions.

Sense Organs. In reptiles, on the whole, the sense of taste is confined to the mouth. The external organs of taste are lacking in this group. This is properly compensated by the better development of the nasal organs, the **olfactory organs** of the chemical sense. The epithelium of the nasal chamber is occupied by olfactory sensory cells. This surface, in some cases is increased by the folding of the wall. In *Uromastix* it is more or less without folds. In reptiles like alligator the lateral wall of each cavity gives rise to an elongated, inwardly projecting ridge called **concha**, which is more or less curled downward. It is supported by thin layer of cartilage or bone belonging to the ethmoid region of the cranium. In *Lacerta* the nasal cavity is provided with an accessory olfactory organ called **vomerolateral organ** or **organ of Jacobson**. It develops as a ventral hollow outgrowth from each nasal cavity, forming a pair of small pouches lying in the anterior region of the roof of the mouth and each opening into the oral cavity by narrow nasopalatine duct. The two ducts open close together just behind the front teeth and anterior to the internal nares.

Eyes. The eyes are large and globular lodged into spacious orbits. There are two complete eyelids having the power of slight movement. When the eyelids close the eyes are drawn inwards. The outer part of the upper eyelids is covered with smaller scales. Normally the lower eyelids is also covered by smaller scales. Under the eyelids a semitransparent **nictitating membrane** is present. It can be pulled across the eye from front to rear. Overhanging each eye there is a fold of skin covered by small scales. This fold is probably protective and the cavity underneath it receives the eye when it is withdrawn. The structure of the eyeball resembles that of the frog. In *Lacerta* and many others the sclerotic is supported from outside by bony sclerotic plates, which do not occur in *Uromastix*. In lizards usually the vitreous contains a vascular protrusion of the nerve head called **pecten**, whose function probably is to provide nourishment to the retina. In *Uromastix* this structure is not developed. The lens is globular and as in reptiles in general the lens is elastic and by the action of the ciliary muscle situated in the adjacent region of the wall of the eyeball the degree of the convexity of the eyeball may be altered.

Ear. The ear consists of two principal parts: the **middle ear** or **tympanum** and the **internal ear** or **membranous labyrinth**. The parts of the labyrinth are usual. The **lagena** is more or less elongated but highly variable in lizards on the whole. The middle ear of lizards is closed externally by the **tympanic membrane** which is lodged in a pit. The anterior edge of the pit presents a dentate appearance. Internally the cavity communicates with the buccal cavity through the **Eustachian tube**. In large species of *Gekko* the tympanic cavity is very large. When caught this lizard opens the mouth widely so that it is possible to see the structure of the tympanic cavity even when the creature is alive. In *Uromastix* also the tympanic cavity is relatively large. Across the upper part of the cavity and bound to it only by a few strands of tissue, passes the bony **columella auris** (cartilaginous in many lizards). It is attached to the tympanum by means of an **extra-columellar cartilage**. The columella is an extremely slender bone with delicate attachments.

The middle ear of agamids (the group to which *Uromastix* belongs) shows degenerative changes. Some of the agamids and others including some species of *Draco* and *Japalura*, there is no visible tympanum, the membrane being covered with skin. Its position is usually indicated by a depression, and on stripping the skin away the tympanum can be seen, together with the attached extra-columellar cartilage. The cavity of the middle ear, when viewed from the pharynx is comparatively large, and columella which crosses it may be exposed, but never completely.

A still later stage in the degenerative process is to be found in *Lyriocephalus*, *Cophotis*, and *Ceratophora*. In these genera the tympanum has gone and the place that it occupied is covered by a muscle, the depressor mandibularis; the extra-columella has gone, or is reduced to a vestige, and the auditory cup is small or is entirely absent; the anterior and posterior processes previously referred to are converted into bone, and unite the columella auris firmly to the quadrate. The cavity of the

tubes. Each continues behind as a narrow convoluted tube, the **vas deferens**, which runs posteriorly and joins the ureter of its side before opening into the cloacal chamber. Thus, the ureter and vas deferens open by a common aperture.

The copulatory sacs or **penes** are two eversible hollow sacs opening into the posterior corner of the cloaca. They are made up of erectile tissues and when everted they become cylindrical. A groove runs to them from the opening of the vas deferens for the conveyance of the sperm. When at rest and withdrawn, the penes form small rounded or longitudinal swellings on either side of the base of the tail, but are rarely distinct. Only one organ is inserted during copulation, but which one is immaterial. This, however, depends upon the side the male happens to be during copulation. How far the form of the organ bears upon phylogeny and classification is still in doubt.

Cloaca. Internally the cloaca is divided into three portions. The rectum and the urinary bladder open into the anterior division (**coprodaeum**) of the cloaca, whereas, in the middle division or **urodaeum** are the openings of the urino-genital ducts. The copulatory sacs can also be seen associated with the posterior portion of the cloaca called **proctodaeum**.

Female. The ovaries (Fig 6.30) are irregular-shaped organs situated in the posterior part of the body cavity, anterior to the kidneys (not as much as the testes). Their upper surface seems studded with rounded protuberances representing the ova. A fold of peritoneum called the **mesovarium** keeps the ovaries attached to the dorsal wall of the body cavity. The oviducts (Fig. 6.30) are two thin-walled tubes whose walls are much folded internally. Anteriorly each tube is wider, much plaited and opens by a longitudinal opening, the **ostium**, facing sideways. They run posteriorly and open, independent of the opening of the ureters, into posterior division of the cloaca. A fold of peritoneum the **mesotubarium** keep the oviduct of each side attached to the body-wall. The cloacal chamber is similar to that of the male but for the fact that the openings of the urinary and genital ducts are separate, and that the copulatory sacs are not developed at all (as in gecko) or are rudimentary.

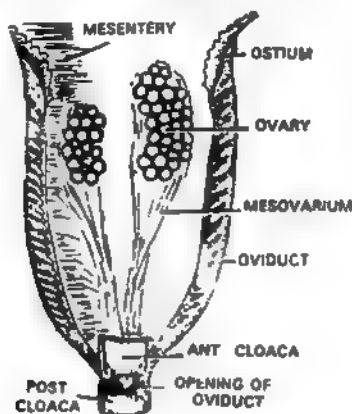


Fig. 6.30. Reproductive organs of the female *Uromastix*.

The egg of *Uromastix* are large measuring 20 by 30 mm. in size, as many as fifteen are said to be laid by a single female. Most lizards lay eggs, but some produce their young alive, and the number of species in which this is known to occur is steadily increasing. In the geckoes and some others the shell contains calcareous dermsits and is brittle, but in others the shell is parchment-like and contains only a small amount of lime. During the incubation period the egg of *Uromastix* and some other lizards

increases in size, slightly, but distinctly. This is because of the absorption of moisture and growth of embryo. For the rupture of the shell the embryo of *Uromastix hardwickii* is provided with a sharp calcareous egg-tooth at the extreme tip of the snout. With the help of this the shell is ruptured and the young one wriggles out. The tooth, however, is shed soon after birth.

Development Because the reptiles have completely given up water their egg has developed complicated structures. The developing amphibian obtains its oxygen and most of its food from the water and excretes its waste matter into the water again, the water also protects it from drying and against mechanical injury. In the reptiles entirely new set of structures have developed for these functions as the water dwelling stage is omitted.

The egg of a reptile or bird contains a large amount of yellow nourishing yolk, which as the embryo grows, is contained in a sac connected with the digestive tract. A large sac, the **amnion**, develops about the body of the embryo. This is filled with liquid and protects the embryo against injury and desiccation (the work done by the natal ponds in the amphibians). From the back end grows out a tube and sac, the **allantois**, in which the waste matter of the body is deposited. The entire egg is protected by a firm shell. The shell is porous. Beneath a portion of the shell lies a membrane pertaining to the allantois and richly supplied with blood vessels. This acts as a respiratory surface taking in oxygen and giving off carbon dioxide. The shell, the yolk sac, amnion and allantois are the structures that satisfy all the needs of the developing organism. There is no need of water for the developing embryo which can now develop directly towards a purely land existence which it assumes soon after hatching.

The cleavage in reptiles and birds is **teloblastic**. In such eggs most of the egg mass consists of inert yolk, while the protoplasm is confined to a small area capping the yolk at the animal pole. Cleavage and blastula formation are confined to this clear protoplasmic area, the yolk does not cleave at all. The first and second cleavages pass through the centre of the animal pole, but they are not complete cleavages of the egg. Additional "equatorial" divisions separate a cluster of cells at the pole from more peripheral members. Further subdivisions, rather irregular, form a **blastodisc** (or blastula). The cell mass tends to be slightly lifted off the underlying yolk, the space formed below is considered to be equivalent to the **blastocoel**. The blastula, however, is a flat sheet and not a sphere.

The potential embryonic regions are distributed over the flat blastodisc as in the shark. Over the periphery the disc is tightly adherent to the yolk. In one region (the future posterior end of the embryo) the margin of the disc is for a time a free growing lip. At this end, as in sharks, cells from the dorsal surface roll inward to the under surface of the disc and extend forward forming a thin sheet of endoderm. Thus a two-layered disc is formed. This is the primary act of gastrulation. The free posterior margin of the disc is comparable to the dorsal lip of the blastopore.

A different procedure is adopted for mesoderm formation. On the dorsal surface of the disc shortly appears the **primitive streak** extending forward from the region of the blastopore lip. It consists of parallel ridges with a groove between them. At the front end of the groove develops a pit, which in many amniotes extends forward and downward as a canal to pierce the roof of the underlying gut cavity. The primitive streak is a region of crucial activity in the formation of the embryo. On the dorsal surface of the disc there is a steady movement of cells medially and posteriorly into the margins of the primitive streak. In the walls of the streak the sheets of cells move downward and then fan outward to interpose themselves between ectoderm and endoderm. Anteriorly, cells taking part in this movement push forward from the pit region to form the notochord; laterally the material moves outward to form the somites and other mesodermal structures. Obviously the primitive streak (although not an open blastopore) functions as a blastopore in forming the mesoderm. The cell-movements which take place here can be compared with those performed by the mesoderm at the blastopore margins in mesolecithal eggs. The primitive streak persists for a considerable period during embryonic development. The development of reptiles, in other ways, is similar to that of the birds.

Relation to Man. The skin of reptiles, chiefly of snakes and lizards, is now exten-

sively used for production of leather, not only as fancy articles for apparel and household use, but also as the upper leather for high-priced shoes. The wearing quality of the reptile leather is greater and they present an infinite variety of pattern. Moreover, the reptile leather can be finished off in any colour. In 1933 India exported about two and three-quarter million reptile skins and ever since the number has steadily increased. Among the lizards the monitor (*Varanus*) skins are shipped usually. Species of *Uromastix* come next, of these, *U. hardwickii* does not appear to be in great demand and *U. asmussi* that is liked abroad is too rare in Indian territory. Its hides are exported from Baghdad.

TYPE KACHUGA

The pond turtles of various genera have long been used as a convenient example for studies of the reptilian characteristics. Several species of *Kachuga* (family Emydidae) occur in the Ganges and other rivers of Northern India. Some species of *Trionyx* and the leathery turtle *Dermochelys* also inhabit fresh water. The group of reptiles including these animals is called the **Chelonians** or **Testudines**. The Testudines is the oldest name available for this group being applied by Batesch in 1788 while *Chelonina* was used by Macartney in 1802.

There is much inconsistency in the use of the words "turtle", "tortoise" and "terrapin". The wholly terrestrial chelonians are generally (but not always) called "tortoises". The marine chelonians are called "turtles", but the commercial "turtle shell" is derived from the marine turtle (*Chelonia imbricata*). Numerous small chelonians, mostly of amphibious habits are indiscriminately called "turtles" or "tortoises". "Terrapin" is applied to various amphibious or aquatic (fresh-water or rarely brackish) chelonians which some persons esteem very highly as food. Here the word turtle is used for aquatic chelonians.

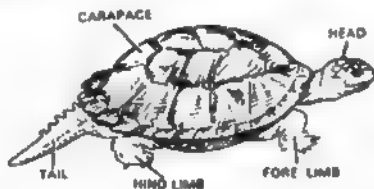


Fig. 6.31. A tortoise

The Chelonians are widely distributed throughout the tropical and temperate zones. The largest living chelonians occur among the marine turtles, some of which weigh hundreds of pounds or even exceed a half-ton. The largest land chelonians are the giant tortoises of the Galapagos Island.

The head is moderate, snout shorter than the orbit, pointed and strongly projecting beyond the lower jaw. The skin of the hinder part of the head is divided into large shields. The digits are fully webbed and the limbs are provided with transversely enlarged scales. The shell of *Kachuga smithi* is pale olive above, the vertebral keel usually blackish. Ventrally the shell is yellow, each shield with a large dark brown patch covering the greater part of it. All the species of this genus are thoroughly aquatic and herbivorous. Their flesh is esteemed as food.

The body of chelonians is generally encased in a bony shell which is their characteristic feature. They are commonly seen sunning themselves on logs along the margins of ponds and rivers. When disturbed they fall into the water with a splash and swim hastily for the deeper parts of the body of water. They are apparently diurnal but they are also known to feed at night. They are not strictly regulated by hours of light and darkness as are other vertebrates. Being cold-blooded they hibernate in winter in temperate regions. They do not show any congregating instinct, although a large number of them may be available in a restricted locality. Each one is totally oblivious

of the presence of all others, except during the mating season, when males seek out the females. Some turtles have been seen to mate at all times from spring to autumn, but the chief mating period occurs soon after the animal comes out of hibernation in the spring. The eggs are laid soon afterwards in a hole or pit in the earth or sand excavated by the female for that purpose. After depositing all the eggs the female covers them and returns to water. It has been experimentally ascertained that a female turtle may lay fertile eggs for as long as four successive years after a single mating.

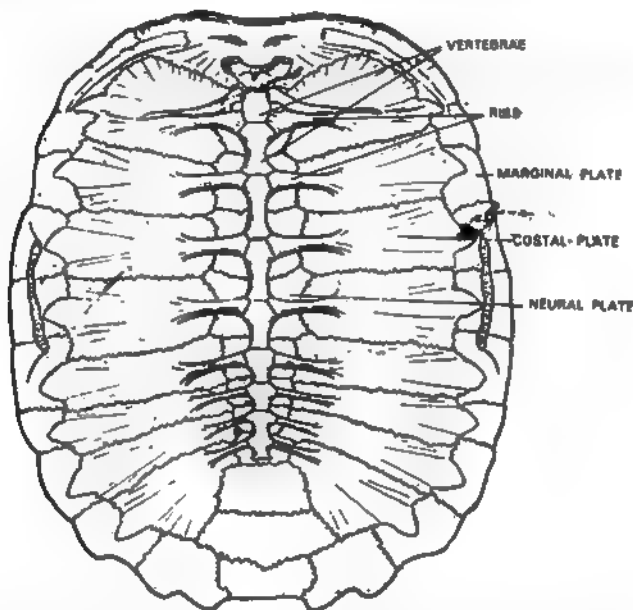


Fig. 6.32. Ventral view of the carapace showing various bony plates, vertebrae and ribs associated with

The longevity of chelonians is proverbial. There is no doubt that some of the giant tortoises have lived for at least 150 years. Nothing is known of the age for which the Indian species live, for a few that have been kept in captivity have not survived long. However, there are authentic records that show that the common European Pond Tortoise *Emys orbicularis* has lived for 70 years and *Testudo graeca* for over 100 years. Most of the oriental tortoises are eaten by the country people.

EXTERNAL STRUCTURE

Shell. The shell of a chelonian consists of a dorsal portion, the carapace, and a ventral portion, the plastron. The carapace consists of a series of median plates, right and left lateral series of costal plates (Fig. 6.32) and usually a series of marginal plates which surround the whole. The median series consists of a large nuchal plate which is anterior and dorsal, usually eight vertebral or neural plates, and usually one to three supracaudal plates. The nuchal plate is not attached to the first dorsal vertebra, above which it lies (Fig. 6.32) but the neural plates are firmly united with the eight dorsal vertebrae below them. Three post-neural (or precaudal or supracaudal) or pygal plates

are visible in the figure from below. There are usually eight costal plates on each side. They are firmly united with the ribs below them, and by their inner and outer extremities with the neural and marginal plates respectively. Usually there are eleven marginal bones on each side and an additional **azygos post-marginal**, which is absent or vestigial in many.

The plastron consists of nine bones, a median **entoplastron** and a pair of **epiplastron**, **hyoplastron**, **hypoplastron** and **xiphiplastron**, beginning from anterior side. The entoplastron is embedded between epi- and hyoplastron plates (Fig. 6.33) and is regarded as the homologue of the inter-clavicle. The epiplastra are regarded homologous with the clavicles, and the remaining elements are modifications of "abdominal ribs". In young tortoises the several plates are separated by large spaces (fontanelles), which are never filled up in some marine and fresh water turtles (*Cheloniidae* and *Trionychidae*), but in most groups they become entirely filled up and in many *Festudinidae* and *Emydidae* the plastron forms one continuous mass (Fig. 6.33). On the sides hyo- and hypoplastral bones are extended to form the bridge through which

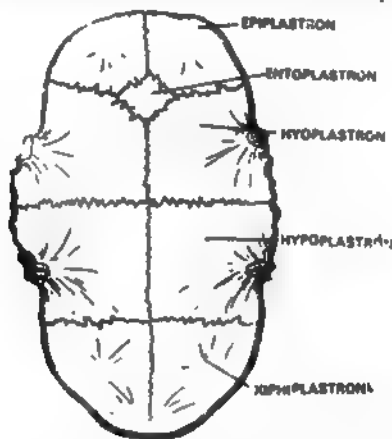


Fig. 6.33. Plastron of a tortoise.

they unite either by suture or by ligamentous tissue with the carapace. In those species which have a bony union the hyo- and hypoplastral bones each send up a process inside the shell, respectively termed the **axillary** and **inguinal buttresses**, which ankylose with marginals and the costal plates. These buttresses are greatly developed in the Indian genera *Batagur*, *Kachuga* and *Hardella*. The processes in these reaching nearly to the vertebrae, form two lateral chambers occupied by the lungs.

Epidermal Shields. The shell (except in the fresh water *Trionychoidea*) is covered with horny epidermal shields, which do not correspond, either in position or numbers with the underlying bony plates. On the carapace there are usually five vertebral, four pairs of costal and twelve pairs of marginal shields. In front of the first vertebral lies the nuchal shields, always small, variable in size and sometimes absent. The last pair of marginal shields may be united to form an unpaired pygal posteriorly. The plastron is also covered with twelve or more shields. They are arranged in six pairs named **gular**, **humeral**, **pectoral**, **abdominal**, **femoral** and **anal** shields from anterior to posterior side. In some an **intergular** (sometimes paired) may be present. In the families *Testudinidae* and *Emydidae* these shields have been reduced in number and are restricted to the anterior and posterior margins of the bridge (the axillary and inguinal shields). In the *Trionychoidea* the bony shell is covered by soft leathery skin.

synapsids. In these there are two typical lateral arches (superior and inferior temporal arches). Such a skull is **diapsid** skull and is found in the group **Diapsida** (*Sphenodon*, crocodilians, etc.). The superior temporal arch (arcade) lies between the superior and inferior fossae. From diapsids arose the first birds. The original diapsid condition has been subjected to further changes. The inferior temporal arch has dropped out in modern lizards, leaving only the superior temporal fossa. Still another condition, **parapsid** condition, exists in a few extinct reptiles (*Plesiosaurs*), wherein only one dorsally situated temporal fossa develops. Whether or not this fossa is equivalent to the superior temporal fossa of diapsids, is not established.

The stem-reptiles, however, did not exhibit such vacuities and arches, hence their skulls are described as **anapsid** (an, without + *apsid*, arch). Among living reptiles chelonians alone lack fossae. For this reason the stem-reptiles and chelonians have been classified together in the sub-class **Anapsida**. Although the skull of a chelonian is of anapsid type yet its roof does not have a fairly complete roofing. There has been considerable excavation from the rear, and numerous elements have been combined both posteriorly and anteriorly, as in specialized skulls. Supratemporal, tabulars, and postparietals are missing and parietals and squamosals have both receded, leaving a wide gap in the temporal region. A postfrontal replaces both postfrontal and postorbital (as in alligators). In addition, a prefrontal may take the place of nasals, lacrimals and prefrontals. It is possible that the postero-dorsal covering may be a restored second roof, the original derm elements having been eroded.

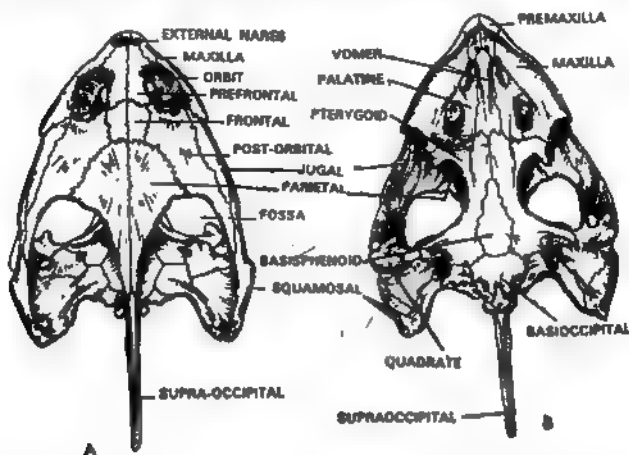


Fig. 6.37. A, dorsal and B, ventral view of the skull of tortoise.

The skull in all the Asiatic chelonians is relatively convex (except in mudturtle *Chitra indica* and *Pelochelys bibroni*). The orbits in these are usually more or less lateral (dorsal in mud-turtles) and each is normally surrounded by five bones, the maxillary, prefrontal, frontal, postorbital and jugal. The alveolar surface of the jaw shows varying breadth, but this is not correlated with feeding habits, as it may be broad or narrow in both carnivorous and herbivorous species. The greatest variation in the skull is shown in the temporal region. In all the primitive forms it was completely or nearly completely roofed over. It is still roofed in marine turtles (*Sphargidae*, *Cheloniidae*). In most Asiatic species the temporal region has become more or less exposed by emargination from behind until only a bar behind the eye (the postorbital arch) and another between the orbit and tympanic cavity (the temporal arch) remain. In some others the temporal arch completely disappears.

and paddle-like in the marine turtles. In all, however, they are typically pentadactyle and complete.

Pectoral Girdle. The pectoral girdle is present but the sternum is absent. Each half of the pectoral girdle consists of two ventral parts and one dorsal part. Of these anterior ventral is a projection from the scapula called the proscapular process (procoracoid bone of many authors). The posterior ventral bone is the larger of the two and is the coracoid. The dorsal bone is elongated reaching the carapace and is called the scapula. All these are cartilage bones. Some membrane bones of the pectoral girdle have fused with the plastron. These are the paired clavicles (epiplastra) and the median interclavicle (entoplastron).

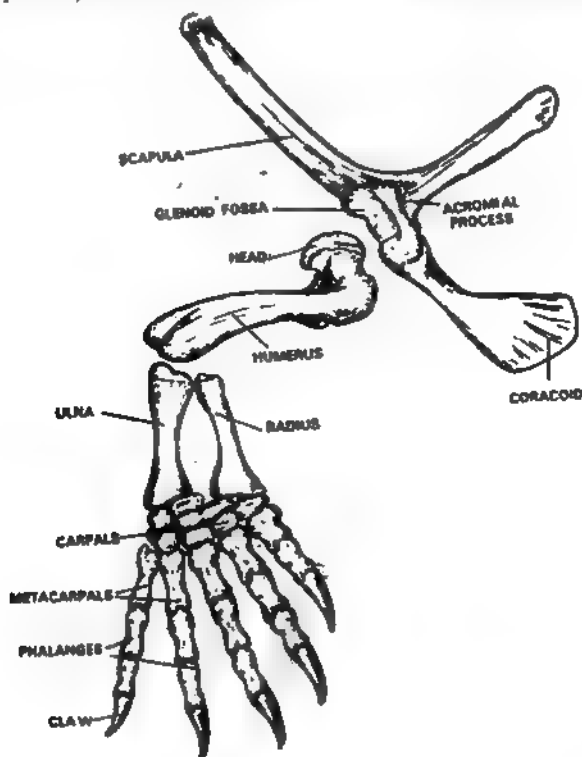


Fig. 6.40. The pectoral girdle and fore-limb of a tortoise.

In general, the bones of the fore-limbs are like those of *Uromastix*. The bones of the carpus or wrist are remarkably primitive in number and position. At the base of the ulna are two bones an outer ulnare and an inner intermedium. The centre of the carpus is occupied by a long bone which is the fused radiale (end at the base of the radius) and the centrale (larger end). Distal to this is a row of five carpals, one for each metacarpal.

Pelvic Girdle. The pelvic girdle of the turtle is a very generalized and representative girdle. It consists of three pairs of bones, two ventral and one lateral and dorsal. The ventral bones consist of a pair of anterior pubes, which meet in the median ventral line forming the *pubic symphysis*, and a posterior pair, the *ischia*, which meet similarly

forming the **ischial symphyses**. These symphyses are composed of cartilage usually missing from dried skeletons. The lateral and dorsal bones of the pelvic girdle are **ilia**, which articulate with the two ends of the two sacral ribs. The pelvic girdle forms an inverted arch completed dorsally by the sacral vertebrae and sacral ribs. Through the arch of the pelvic girdle pass the terminal portions of digestive and urogenital systems. Between the pubis and ischium of each side is enclosed the large **obturator foramen**, through which pass nerves and blood vessels. The two obturator foramina are completely separated in life by a cartilage which bridges the space between the pubic and ischial symphyses. Attached to the anterior extremity of the pubic symphysis is the **epipubis**. Each pubis has a prominent **lateral pectineal process**, projecting forward. The **acetabulum** is formed at the junction of pubis, ischium and ilium (Fig. 6.41).

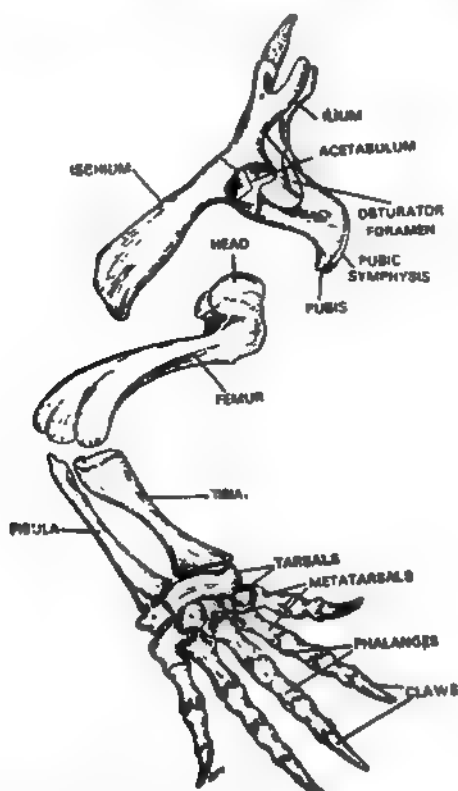


Fig. 6.41. The pelvic girdle and hind-limb of a tortoise.

The hind-limb consists of all the bones present in the limb of *Uromastix*. The thigh consists of a large bone, the femur, the head of which fits into the acetabulum. The shank comprises the tibia and fibula (smaller). Ankle is made up of five (or six) bones. At the bases of the tibia and fibula is a large transversely elongated bone (formed of four fused bones, *tibiale*, *intermedium*, *centrale*, *fibulare*). *Fibulare* may be separate in some. This is followed by a row of four bones, the **tarsals** (numbered from the

preaxial, tibial, side to the postaxial, fibular, side). The apparent fourth tarsale is really the fused fourth and fifth tarsale. This row is followed by five metatarsals and beyond these are the digits composed of bony joints or **phalanges** terminating in horny claws. There are two phalanges to the first digit and three to all of the others. It is noteworthy that in the turtle (and reptiles in general) the movement of the foot upon the leg occurs between the two rows of the tarsal bones, i.e., it is an **intratarsal joint**.

COELOM AND VISCERA

Coelom. On removing the plastron, a membrane, the **parietal membrane** is exposed. This covers and conceals the viscera. The muscle layer which is normally present between the skin and peritoneum is completely lacking in the ventral wall of the tortoise. The ventral wall, therefore, consists of the skin with its contained exoskeleton

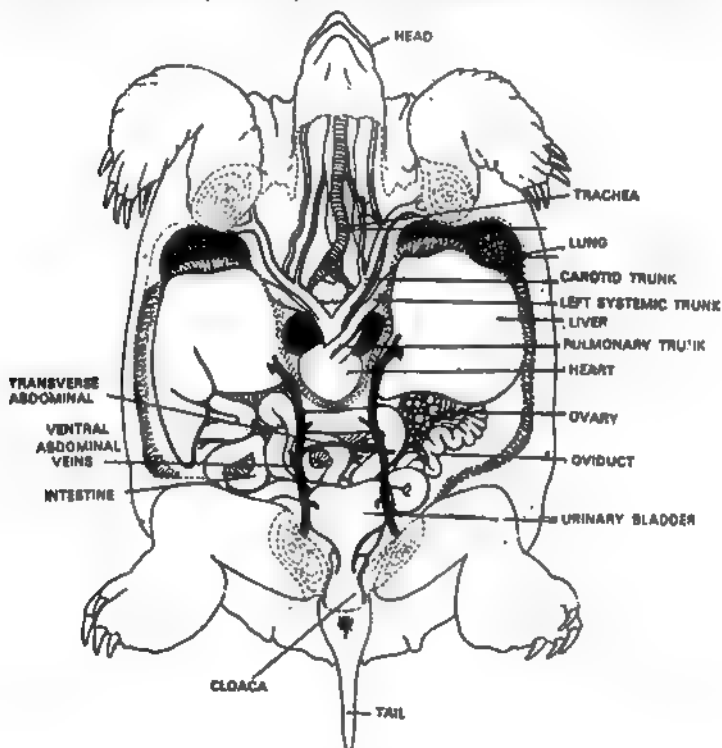


Fig. 6.41. Coelom and viscera of *Kachuga*.

and the peritoneum. In the median line, in the anterior part of the parietal peritoneum, posterior to the pectoral girdle, is situated the **pericardial sac** enclosing the heart. The heart in this case is more posterior than in the amphibians and lizards. The space between the pericardial sac and the heart is the **pericardial cavity**, a portion of the coelom. The conspicuous **ventral abdominal veins** run longitudinally in the parietal peritoneum between the pericardial sac and the pelvic girdle. Below them lies the large **pleuroperitoneal cavity**, whose walls are lined by the parietal peritoneum. In other

forms studied so far the pericardial cavity is anterior to the pleuroperitoneal cavity and separated from the latter by the transverse septum, in the tortoise the pericardial cavity is ventral to the pleuroperitoneal cavity and the transverse septum seems to have disappeared.

Viscera. The anterior part of the pleuroperitoneal cavity is occupied by the large brown liver on each side of the heart. Posterior to the liver are the coils of the intestine. In female specimens the ovaries containing eggs of various sizes are conspicuous objects in the lateral and posterior part of the pleuroperitoneal cavity. Running alongside each ovary is the coiled oviduct. Just in front of the pelvic girdle is the large bilobed urinary bladder.

The liver consists of right and left lobes whose lateral margins curve dorsally to fit in the curves of the carapace. The pericardial sac rests in a depression between the two lobes. The latter are united by a narrow bridge passing dorsal to the heart. Posterior to the heart the liver is united to the parietal peritoneum by very short mesenteries corresponding to the falciform ligament of other vertebrates. In these mesenteries the ventral abdominal veins leave the peritoneum and pass into the liver. The parietal peritoneum passes along the dorsal face of the pericardial sac, to which it is inseparably fused. This compound membrane between the heart and liver is the transverse septum, which has assumed an oblique position, owing to the descent of the heart (Fig. 6.42). The ventral (original anterior) face of the septum is as before, part of the wall of the pericardial cavity, the dorsal (original posterior) face forms part of the parietal peritoneum. The liver is, as usual, attached to the transverse septum by the coronary ligament. On the posterior face of the pectoral girdle the parietal peritoneum turns dorsally and passes to the carapace of which it forms the inner lining. Finally, it curves dorsally, following along the anterior surface of the pelvic girdle, and passes to the inner surface of the carapace.

The elongated stomach curves dorsally to the lateral border of the left liver lobe. Anteriorly, the narrow oesophagus enters the stomach (Fig. 6.43). The stomach passes along the dorsal surface of the left lobe of the liver to the middle of which it is attached along its entire length by the short gastrohepatic ligament. About opposite the bridge connecting the two lobes of the liver, the stomach passes insensibly into the small intestine, the first part of which is the duodenum. The duodenum is united to the middle of the dorsal surface of the right lobe of the liver by the hepatoduodenal ligament. In this ligament is situated a long white gland, the pancreas. About one-quarter of an inch back of the right end of the pancreas, a pancreatic duct passes from the pancreas into the duodenum and may be revealed by picking away the substance of the pancreas at this point. On the dorsal surface of the right lobe of the liver near its lateral border is the large gall-bladder, which is connected to the duodenum by a short but stout bile duct. Beyond the entrance of the bile duct the small intestine turns sharply posteriorly and is then thrown into a number of coils. The dorsal mesentery attaches it to the median dorsal line of the coelom, this part of the dorsal mesentery is the mesentery proper. Portions of it also support the duodenum and the stomach, named mesoduodenum and mesogaster, respectively. The mesoduodenum is fused to the hepatoduodenal ligament so that the two appear as one, but the mesogaster is distinct from the gastrohepatic ligament. On the right the intestine merges into the large intestine or colon. At the junction of the small and large intestine is a slight projection, the caecum. The colon generally crosses the pleuroperitoneal cavity transversely and then turns posteriorly and runs straight caudad to the cloaca. The mesocolon, a part of the mesentery, supports the colon. In the mesocolon on the dorsal side of the colon, shortly beyond the caecum, is a rounded red body, the spleen. At a point ventral to the colon will be found the large, thin-walled, bilobed urinary bladder. It is generally greatly distended with urine but in some specimens may be contracted to a small mass. The bladder has no ligaments, the peritoneum leaving the body wall around the stalk of the bladder and passing over its surface to form its visceral investment. Posteriorly the large intestine passes into a tube, the cloaca, which proceeds dorsal to the girdle to the anus. At the point of entrance of the large intestine into the cloaca the urinary bladder is attached to its ventral surface by a stalk. On each

gill-arches. On each side of the roof of the pharynx posterior to the muscles which connect the skull and lower jaw, is the opening of the auditory or Eustachian tube, a canal which leads from the pharynx to the cavity of the middle ear. The auditory tube and also the cavity of the middle ear are outgrowths from the first visceral pouch. Posteriorly the pharynx narrows into the oesophagus.

The trachea or windpipe is a tube stiffened by rings of cartilage lying in the median line of the neck. In front of the place where trachea emerges from the pharynx lies the hard body of the hyoid, with its two pairs of horns extending posteriorly. The hyoid and its horns are derivatives of the second, third and fourth gill-arches. The larynx is an expanded chamber at the anterior end of the trachea. The lateral walls of the larynx are supported by two arytenoid cartilages, small cartilages supporting the two triangular flaps which enclose the glottis between them. Posterior to the glottis is a ring-shaped cartilage, the cricoid, which is much wider on the ventral than on the dorsal side. The arytenoids probably are remnants of the fifth gill-arches, while the cricoid is the enlarged first cartilage of the series of rings in the trachea.

Lying dorsal to or to one side of the trachea there is a soft tube, the oesophagus. The trachea runs posteriorly and just anterior to the heart the trachea bifurcates into the two bronchi which proceed to the lungs lying dorsal to the liver lobe and stomach, against the carapace. Each lung is a large spongy organ into which runs a bronchus accompanied by a pulmonary artery and a pulmonary vein. The lung is extremely spongy as seen from within, cords of connective tissue divide the interior into the air spaces or alveoli. The lung lies in the pleuro peritoneal cavity and the parietal peritoneum passes over the ventral surface of the lung leaving it outside of the membrane. Such a relation to the peritoneum is spoken of as *retroperitoneal*. The posterior end of the lung, however, projects into the pleuroperitoneal cavity and is clothed with the peritoneum.

The path followed by the air in respiration is; external nares, nasal cavities, internal nares, mouth, pharyngeal cavity, glottis, larynx, trachea, bronchi and lungs. In the pharyngeal cavity the paths of food and air cross.

CIRCULATORY SYSTEM

Heart. The heart of the tortoise is three chambered. It lies in the pericardial cavity. It has usual chambers, the thick-walled posterior conical chamber the *ventricle*, and two thin-walled *auricles* both of which are completely separated from each other. The ventricle is attached to the posterior pericardial wall by a ligament, which is apparently a remnant of the ventral mesentery or ventral mesocardium of the heart, a structure which was considered in the general discussion of coelom. A large chamber, the *sinus venosus*, is situated dorsal to the auricles and attached to the right auricle. The large bases of the systemic veins are seen entering the sinus. Several large vessels (arteries) spring directly from the base of the ventricle without the intervention of a *conus arteriosus* which is lacking, or to be very accurate, is reduced so much as to be invisible. The base of the arteries which spring from the ventricle correspond to the ventral aorta of elasmobranchs. The ventral aorta is, thus, seen to have split into several separate trunks.

Internal Structure. The posterior chamber of the heart (Fig. 6.44) is the *sinus venosus* which receives the four great systemic veins. It is a thin-walled chamber attached to the right auricle, into which it opens by the *sinus-auricular opening* guarded by a pair of thin valves. The walls of the auricles are somewhat spongy. A thin interauricular septum separates completely the cavity of the left auricle from that of the right one. The opening of the pulmonary veins is situated in the dorsal wall of the left auricle near the septum. The auricles open into the ventricles by large *auriculo-ventricular openings*. The walls of the ventricle are thick with the muscular columns projecting into the interior. The cavity of the ventricle is a broad but flattened cavity usually containing a spongy network. In the base of the ventricle there is a band passing across from one side to the other. On each side of this band is an *auriculo-ventricular opening*. The band is a continuation of the interauricular septum and forms a fold or valve on each side, which partially occludes the *auriculo-ventricular*

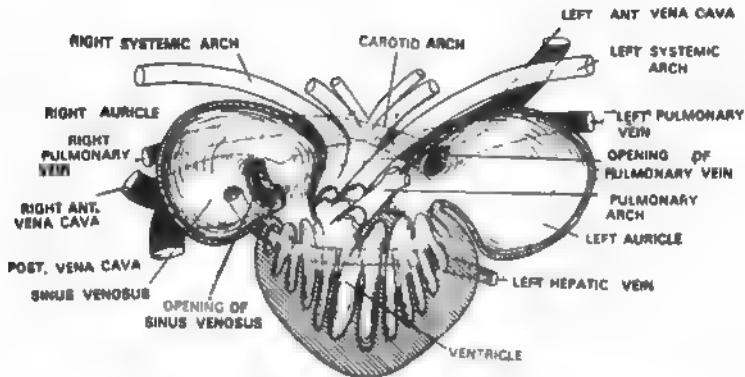


Fig. 6.44. Sagittal section of the heart of tortoise

opening. The right valve continues ventrally into a ridge which is on the ventral flap. This ridge is the incomplete interventricular septum. The interventricular septum separates the ventricular cavity into two and a space is left dorsal to the septum by which the right and left ventricles communicate with each other. The right ventricle to the right of the septum is very small while the left ventricle is much larger and communicates with the cavity of both auricles owing to the incomplete character of the interventricular septum. The pulmonary artery opens into the ventricle, ventral to the interventricular septum. The opening of the left aorta is to the right of the interventricular septum, into the small right ventricle; while that of the right aorta is to the left of the septum, into the left ventricle, however, owing to the gap, dorsal to the septum, the left aorta can also obtain blood from the left ventricle. Small pocket-like semilunar valves guard their exits from the ventricle. They represent the remains of the *conus arteriosus*.

Veins. Running in the ventral peritoneum from the pelvic girdle upto the heart are two large veins, the **ventral abdominal** (Fig. 6.45). They are homologous with lateral abdominal veins of elasmobranchs. The two veins are generally connected just anterior to the pelvic girdle by a cross-branch. They receive pericardial veins from the pericardial sac and then each turns dorsally to enter the liver. Just at this turn each vein receives a **pectoral branch** from the pectoral muscles of that side. Finally each abdominal vein reaches the liver and penetrates its lobes.

As the ventral abdominal veins run posteriorly they receive several small veins from different organs. The small **vesical vein** passing from the bladder into each abdominal vein is one from the urinary bladder. After this each abdominal vein passes to one side of the pointed anterior extremity of the pelvic girdle and at the same time gradually turns laterally. As it turns it receives a **pelvic vein** which runs over the ventral surface of the muscles of the pelvic girdle. The left pelvic vein seems to be usually larger than the right one. Between the heart and pelvic girdle each vein gives off laterally one or more small branches which pass to the borders of the carapace, where they join the **marginocostal vein** to be described later.

The two abdominal veins have identical branches as such it is necessary to follow only one. Each passes along the dorsal surface of the pelvic girdle near the anterior margin of the latter. Just beyond the pelvic vein a small **crural** from thigh muscles and a larger vein from fat enter the abdominal. About an inch-and-a-half lateral to this the large **femoral vein** emerges from the leg and joins the abdominal vein, now designated the **iliac vein**. The femoral vein enters into the leg. The iliac vein is now situated alongside a conspicuous artery, **epigastric artery**, both being embedded in the abdo-

minal wall from which small veins pass into the iliac vein. After a short distance the iliac vein receives the **epigastric vein** which accompanies the artery of the same anteriorly along the curve of the carapace. The iliac vein now turns abruptly posteriorly and runs between the base of the leg and the carapace, deeply embedded in some loose tissue. It receives branches from the carapace and near the posterior part of the thigh a well-marked **sciatic vein** from the thigh. Posterior to this point it receives several small branches from the leg as the caudal vein passes along the side of the tail, receiving at the base of the tail a cloacal branch from the anal region (Fig. 6.45).

At the place where the epigastric vein enters the iliac vein, a large vein continues forward from the anterior and dorsal surface of the iliac. This vein, the **renal portal vein**, runs forward and dorsally, penetrates the pleuroperitoneum. The renal portal vein runs from the point where it leaves the iliac through the pleuroperitoneum toward the kidney. Before reaching the kidney it receives a vein from the carapace. At about the middle of the lateral border of the kidneys is a fissure; the renal portal vein enters this fissure and passes on to the ventral face of the kidney where it immediately forks. One of its branches, the **vertebral vein**, runs forward and passes anteriorly dorsal to the arches of the ribs and receives laterally an **intercostal branch** at each suture between the costal plates of the carapace. The intercostal veins anastomose with each other in the curve of the carapace by means of a longitudinal vessel, the **marginocostal vein**, which is the anterior continuation of the epigastric vein previously noted. The marginocostal vein also has connections with the abdominal veins. The posterior branch of the renal portal vein passes posteriorly over the ventral face of the kidney and as the **internal iliac** or **hypogastric vein** receives branches from the reproductive organs (male), bladder, cloaca, etc. The renal portal vein in its passage along the ventral face of the kidney gives off branches into that organ. The renal portal vein is the posterior part of the **posterior cardinal vein**. The vertebral vein is formed by the longitudinal fusion of segmental branches of the posterior cardinal vein of the embryo.

In the turtle the ventral abdominal veins have formed a connection with the renal portal system posteriorly, while anteriorly they enter the liver instead of the cardinal system, while in the elasmobranchs the case is entirely different.

Hepatic Portal System. Below the stomach and duodenum at the place where the gastro-hepato-duodenal ligament is attached to the liver lies a large vein, the **hepatic portal vein** (Fig. 6.46). It runs completely across the liver embedded in its wall, and at the right, at the point where the bile duct enters the duodenum, turns abruptly posteriorly, penetrating the mesentery. On the left there are numerous gastric veins entering the hepatic portal vein from the stomach. Just to the right of the bridge connecting the two lobes of the liver, two or three anterior pancreatic veins pass from the pancreas into the hepatic portal vein. Near the bile duct it receives **cystic vein**, from the bile duct, posterior pancreatic veins from the right end of the pancreas, and a long **duodenal branch** from the first part of the small intestine. Posteriorly it is embedded in the pancreas and at the bend of the duodenum penetrates the mesentery and emerges to the left of the duodenum. The vein next passes to the posterior side of the adjacent loop of the small intestine, then passes on the left side of the spleen in contact with that organ and finally receives numerous splenic tributaries from it. Shortly posterior to the spleen the hepatic portal vein reaches the central point of the mesentery. At this place the numerous mesenteric veins, accompanied by arteries, pass in the hepatic portal vein from all parts of the intestine. In the substance of the liver the hepatic portal vein breaks up into many branches. As in other vertebrates the direction of flow in the hepatic portal vein is from the digestive system into the liver.

Four large systemic veins enter the sinus which is not symmetrically placed but is displaced slightly to the right, connecting with the right auricle. A large vein enters the left wall of the sinus passing around the border of the left auricle. This is the **left precaval vein** (also called anterior vena cava and descending vena cava). Another vein, the **left hepatic vein**, emerges from the bridge of the liver and enters the left angle of the posterior wall of the sinus. The very large vein which passes into the right angle of the posterior wall of the sinus is the **postcaval vein** (also named posterior vena cava and ascending vena cava). It emerges from the right lobe of the liver. Just in front of the

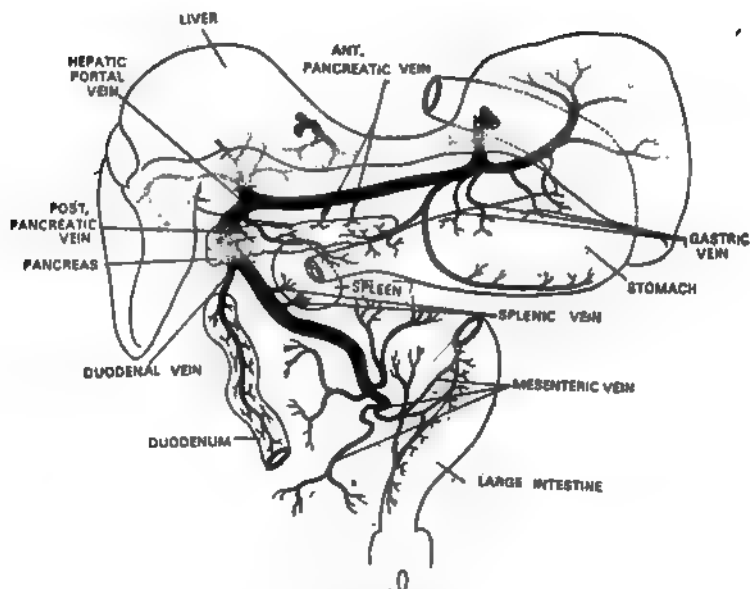


Fig. 6.46. Hepatic portal vein of the tortoise.

shoulder. Here it is seen to be formed by the union of two large branches, the external jugular vein from the neck and the brachial from the fore limb. The external jugular lies along the side of the neck, lateral and dorsal to the internal jugular. It collects from the head, and in its passage posteriorly along the neck receives at regular intervals vertebral veins from between the vertebrae. Near its junction with the brachial it receives the last of the vertebral veins which descends from the junction between last cervical and first trunk vertebra. The external jugular vein also receives branches from the skin and muscles of the shoulder region. The fourth and most lateral and dorsal of the tributaries of the precaval is a small scapular vein which comes from the muscles covering the scapula.

Each precaval receives a hepatic vein from the liver lobe of its side. The postcaval runs anteriorly along the dorsal aorta and enters the substance of the liver from which small hepatic veins enter into the postcaval. The postcaval is formed of two vessels running along the medial side of the kidneys. Each of these receives numerous renal and genital veins from the kidney. A pulmonary vein passes from each lung to the left auricle of the heart. It is situated posterior to the bronchus and passes dorsal to the precaval veins. Both the right and the left pulmonary veins join at the entrance into the left auricle, near the left precaval vein.

Arteries. Three large arterial trunks (Fig. 6.47) extend forward from the ventricle. These vessels have been derived from the ventral aorta which splits into three. The trunk farthest to the left is the pulmonary artery, the vessel next to it is the left aorta, the third and right-hand trunk is the right aorta. The right is concealed from view by the large branch, the brachiocephalic (innominate) artery which it gives off immediately on leaving the heart. From the base of the brachiocephalic artery arise small coronary arteries and branch over the surface of the heart. The brachiocephalic artery lies in the median line and forks at once into large branches. In the angle of the fork lies a reddish thyroid gland.

The brachiocephalic artery divides into four trunks the large medial ones are the right and left subclavian arteries, the much smaller lateral ones are the right and left carotid arteries. The two subclavians embrace the thyroid gland between their bases and supply small thyroid arteries into this gland. Each subclavian next gives off branches to the ventral side of the neck and to the trachea, of which the chief one is the ventral cervical artery, a vessel arising from the subclavian about one-half inch beyond the thyroid gland and branching profusely into the oesophagus, trachea, muscles of the neck, and thymus gland. The thymus gland is a yellowish mass lateral to the ventral cervical artery and receiving branches from it. The subclavian artery now named the axillary, turns laterally and passes to the inner surface of the pectoral girdle, where a large branch arises and branches extensively into the pectoral and shoulder muscles. The axillary then turns abruptly posteriorly and about an inch beyond the turn gives off the small dorsal cervical into the neck, the first inter-costal laterally, and the vertebral caudally. The first intercostal runs laterally and then turns posteriorly, joining the margino-costal artery, which courses along the curve of the carapace. The vertebral passes backward along the vertebral column dorsal to the ribs alongside the vertebral vein and gives off at the sutures of the costal plates the inter-costal arteries, which run laterally into the margino-costal artery. At the point where the first intercostal and vertebral arise, the axillary bends sharply laterally and as the brachial artery passes into the fore limb alongside the brachial vein.

Each carotid artery passes forward along the ventral side of the neck, soon crossing dorsal to the subclavian and then coming to lie medial to the subclavian. As the carotid artery passes the thymus gland it gives branches into the gland. It then proceeds, without branching, the entire length of the neck in contact with internal jugular vein and the vagus nerve, and enters the skull by a foramen in front of the auditory region.

The pulmonary artery is the one farthest to the left of the three arterial trunks which arise from the ventricle. It divides immediately into right and left pulmonary arteries. The left pulmonary proceeds laterally posterior to the left aortic arch, to which it is more or less bound by connective tissue, forming the arterial ligament or ligament of Botallus. The pulmonary proceeds directly to the lung in company with the bronchus and left pulmonary vein. The right pulmonary artery courses to the right lung almost in the same way.

Each of the aortic arches makes a curve as it leaves the heart and turns posteriorly, passing dorsal to the precaval vein, the bronchi and pulmonary vessels and dorsal to the lobes of the liver. The left aorta passes down to the left of the oesophagus and dorsal to the stomach. It gives off simultaneously three large branches. One is the gastric artery which passes to the stomach in the cardiac region. After a short distance it forks into anterior and posterior gastric arteries which supply the lesser and greater curvatures of the stomach respectively. Another branch from the left aorta is the coeliac artery. It soon forks into anterior and posterior pancreatico-duodenal arteries. The anterior pancreatico-duodenal artery passes to the left end of the pancreas, gives off three branches into pyloric end of the stomach and to the liver, then turns to the right and runs along the pancreas supplying the liver, pancreas and duodenum with many small branches. The posterior pancreatico-duodenal artery enters the right end of the pancreas and passing along the pancreas supplies branches to the liver, pancreas, duodenum, and gall bladder. The third branch of the left aorta is the superior mesenteric artery. It runs posteriorly in the mesentery. At this point the artery breaks up in a fan-like manner into many radiating branches. One branch, the inferior mesenteric, passes to the large intestine and accompanies it to the cloaca (Fig. 6 47).

The left aorta curves dorsally (Fig. 6 47) and posteriorly and very soon meets another vessel coming from the right. The two join in a V-shaped manner and form one vessel, the dorsal aorta, which continues posteriorly in the median dorsal line. The dorsal aorta runs in the median line ventral to some long muscles and in company with the postcaval vein which courses at first to its right and later comes to lie ventral to the aorta. The aorta gives off a number of small branches into the muscles on which it rests and then passes between the two kidneys. It gives numerous renal arteries into the kidneys and genital arteries to the reproductive system. At the posterior end of the kidneys it forks into the right and left common iliac arteries.

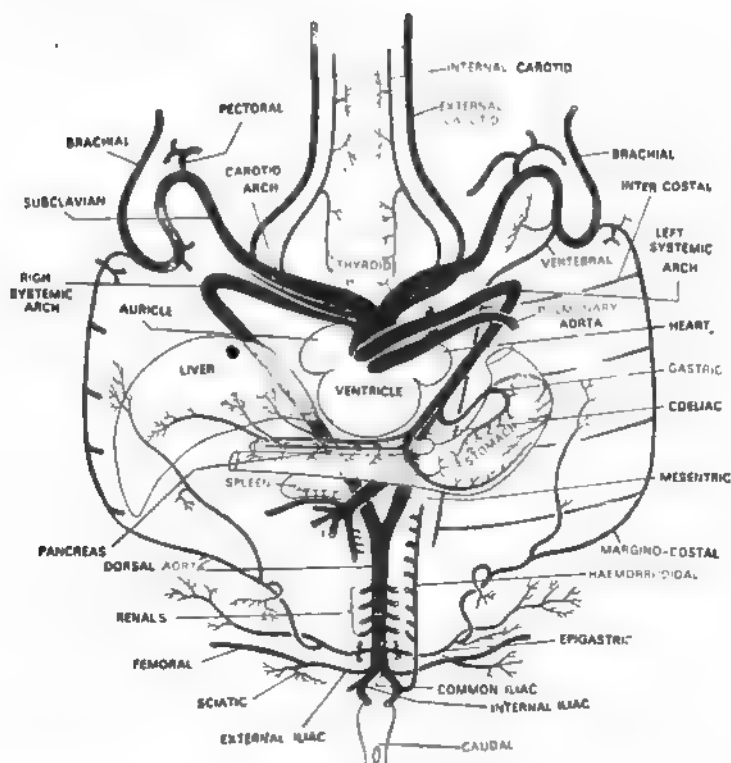


Fig. 6.47. The arterial system of a tortoise.

Two large arteries emerge dorsal to the kidney. The anterior one is the **epigastric artery**; the posterior one, the **common iliac**. It runs laterally to the point where the renal portal vein enters the pleuroperitoneal cavity. At this point it divides. The anterior branch continues to the carapace and runs forward along the curve of the carapace supplying the fat bodies and becoming continuous with the **marginocostal artery** described above. The posterior branch turns and passes medially parallel to the ventral abdominal vein. It supplies the base of the leg and the pelvic muscles and terminates on the ventral surface of the pelvis.

The **common iliac artery** divides at once before it has emerged from above the kidney into an **internal iliac** and an **external iliac** artery. The **external iliac** forks after a short distance. The medial and larger branch supplies the muscles of the pelvis and as the **femoral artery** enters the thigh. The smaller and lateral branch passes deep dorsally to the point where the ilium is articulated to the sacral ribs; here it passes dorsal to a nerve and turns ventrally as the **sciatic artery** into the hind leg, running along the medial surface of the ilium. The chief branch of the **internal iliac** is the **hemorrhoidal artery** which passes forward along the side of the large intestine; in addition there are branches to the bladder, the reproductive organs, and the pelvic region in general.

Course of Circulation. All the venous blood returns to the sinus venosus which opens in right auricle, which passes it on into the right side of the ventricle. Although

lies just behind the chiasma, with the hypophysis projecting ventrally. The roots of the cranial nerves arising from the ventral surface of the medulla are also visible. Notable among these are shown in Fig. 6.48.

Ventricles. A study of a median sagittal section reveals the usual ventricles in the turtle brain also. The fourth ventricle (Fig. 6.49) in the medulla, the aqueduct or passage below the cerebellum, optic ventricle in the optic lobe, the third ventricle in the diencephalon. The size of the diencephalon is increased as compared with the elasm-

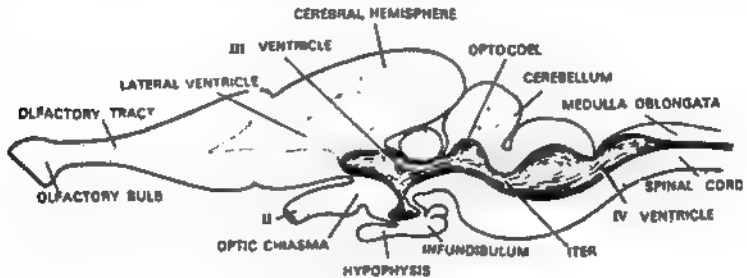


Fig. 6.49. Median sagittal of the brain of tortoise.

branch, and there is the backward extension of the cerebral hemisphere over the diencephalon. The diencephalon is divided into *epithalamus*, *thalamus* and *hypothalamus* as in the dogfish, each including the parts previously enumerated. The cerebral hemisphere presents a solid medial wall, called the *septum*. The cavity of the cerebral hemisphere is the *lateral ventricle*, and a large mass protrudes from the floor into the ventricle. This is the *corpus striatum*.

The function of the parts of the turtle brain are similar to those mentioned for the elasmobranch brain. The cerebral hemisphere is still largely olfactory, although its lateral surface is beginning to assume the functions characteristic of the mammalian hemisphere.

Cranial Nerves. There are twelve pairs of cranial nerves. The first ten pairs have the same name and similar disposition as found in other vertebrates. The *spinal accessory* (or eleventh) arises along with the *vagus* (tenth) by a number of roots from the side of the medulla. Of these roots the more anterior ones are those of the *vagus* and the posterior ones are of the *spinal accessory*. Ventrally to the roots of these nerves are situated the roots of the *hypoglossal* (twelfth) nerve. The three nerves pass out from the skull together.

Spinal Nerves. There is a pair of nerves corresponding to each vertebra and there are usual two plexi. There are nine pairs of cervical nerves. The *brachial plexus* is generally formed by the cross unions between the ventral rami of the last four cervical spinal nerves and the first dorsal spinal nerve (of the trunk). The four cervical nerves form a complex net work on the surface of the shoulder muscles. From this network the large median nerve proceeds to the fore-limb.

Each nerve of the trunk is called *dorsal*, which in most cases is divided into two branches, a smaller *dorsal ramus* and a larger *ventral ramus*. A large ganglion, the *dorsal spinal ganglion*, situated in contact with the centre of the centrum, gives off the nerve branches. In all there are seven dorsal nerves of this type. The ventral rami of the eighth, ninth and tenth dorsal nerves together with the two sacral nerves form the *lumbosacral plexus* for the hind limb. The two sacral nerves receiving also a contribution from the tenth dorsal nerve form a trunk, the *sciatic nerve* situated among the muscles of the posterior side of the leg. There is a *caudal nerve* corresponding to each caudal vertebra.

Sympathetic System. The sympathetic trunk is bound with the *vagus* running along the side of the neck but at about the level of the first nerve of the *brachial plexus*,

most probably, is meant to attract members of the opposite sex. The individuals leave a trail of scent in the waters they inhabit. In typical land species (Testudinidae) the glands are not present. Whether the secretion is cyclical in amount or intensity is unknown. These glands are more odoriferous in some (the American Muskturtles) than in others. Asiatic species *Geoemyda trijuga* produces strong odour. The scent-glands are small, like fat-bodies, with fine duct discharging their contents on the surface of the body. The ducts pursue somewhat tortuous course and usually pierce through the bone to open. The openings are very minute round or slit-like (they are seen with difficulty). The glands that open in the axillary and inguinal shields themselves, or in the soft skin adjacent to them are called **axillary** and **inguinal glands**. The gland opening on the margin of the carapace, above the forelimb, is the **humeral gland**.

Female. The urogenital system of female consists as usual, of a pair of kidneys with ducts, a pair of ovaries and a pair of Müllerian ducts or oviducts.

The kidneys of the turtle are metanephric. They are flattened lobed organs fitting snugly against the posterior end of the pleuro-peritoneal cavity. The renal portal vein and its tributary the internal iliac, run along the ventral face of each kidney. Directly dorsal to it is a tube, the **metanephric duct** or **ureter**, extending from the middle of the kidney to the cloaca (Fig. 6.50). It enters the cloaca at the base of the thickening caused by the oviducal entrance.

The ovaries are large bag like bodies in the posterior part of the pleuroperitoneal cavity (Fig. 6.50). They usually contain yellow eggs in various stages of development. Each ovary is supported by a mesentery, the **mesovarium**. Along the posterior border

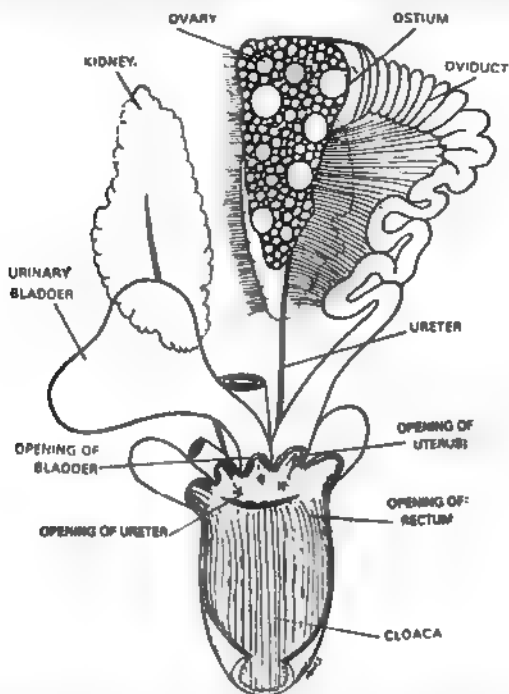


Fig. 6.50. Female genital organs of a tortoise. Unlabelled diverticula on the sides of the cloaca are the anal sacs.

of each ovary runs the oviduct, a large white coiled tube, supported by the *mesotubarium*. The ostium lies in the mesentery in the anterior part of the body and has wing-like borders which are generally closed together and have to be spread apart to see the opening. Posteriorly each oviduct opens into the side of the anterior end of the cloaca ventral to the opening of the intestine. The stalk of the large bilobed urinary bladder joins the cloaca midway between the two oviducts.

The cloaca lies under the pelvic girdle normally. Attached to each side of the cloaca, posterior to the oviducts, are two elongated sacs, the *accessory urinary bladders*. Their function is unknown but is possibly respiratory or hydrostatic. A dark structure visible through the wall of the cloaca is the *clitoris*, homologous with the penis of the male. It is of no use in the female. The *clitoris* consists simply of the thickenings in the ventral wall of the cloaca. The large openings of the accessory bladders lie in the side of the cloaca. The opening of large intestine is the most dorsal of the openings and is somewhat separated by a fold from the urogenital openings. Ventral to the opening of the intestine are the openings of the oviducts on thickened papillae. Between and ventral to the oviducal openings is the opening of the urinary bladder.

Male. The male urogenital system consists of the paired kidneys, paired testes and their ducts. The ducts of the testes are the Wolffian ducts now called the *vasa deferentia*.

Kidneys. The kidneys (Fig. 6.51) are flattened lobed bodies fitting against the posterior wall of the pleuroperitoneal cavity. The kidneys are metanephric, and their ducts are the metanephric ducts or ureters. The ureter lies immediately to the dorsal side of the epididymis. The ureter is short tube proceeding to the cloaca, into which it opens just anterior to the opening of the vas deferens. The openings lie at the sides of the anterior beginning of the urethral groove in the cloaca. The cloaca has two accessory bladders attached to its lateral walls as in the female. The rectum opens into the cloaca dorsally and the urinary bladder is ventral through the ventral wall of the cloaca a dark mass is seen. This is the *penis*, the organ of copulation. A rounded mass projects from the anterior wall of the cloaca to either side of the stalk of the bladder; constituting parts of the penis called the *bulbs* of the *corpora cavernosa*. Muscles which retract the penis are attached to the ventral wall of the cloaca.

Testis. Each testis (Fig. 6.51) is a yellow spherical body attached to the ventral face of the kidney by the *mesorchium*. Lateral and posterior to the testis is an elongated, dark-coloured coiled body, the *epididymis*. The testis is connected to the anterior part of the epididymis by the minute *vasa efferentia* which run in the *mesorchium*. The *vasa efferentia* and this portion of the epididymis are the remnants of the *mesonephros*. The remainder of the epididymis constitutes the male duct or *vas deferens* (Wolffian duct). Posteriorly each *vas deferens* enters the cloaca anterior to and at the base of the bulb of the penis.

The penis consists of two spongy ridges the *corpora cavernosa* or *cavernous bodies*, in the ventral wall of the cloaca. Between these folds in the midventral line is a deep groove, *urethral groove*, which in the natural condition is practically converted into a tube by the approximation of the cavernous bodies. The urethral groove terminates caudad at the base of a heart-shaped projection, the *glans* of the penis. The anterior ends of the cavernous bodies form the bulbs already noted, which project forward into the coelom at the sides of the stalk of the bladder. The bulbs are filled with blood which they receive from the internal iliac vein. All parts of the penis are highly spongy and vascular. In the sexual act the blood from the bulbs rushes into the spongy spaces of the cavernous bodies and the glans, erecting them, and causing the cavernous bodies to come in contact above the urethral groove, converting the latter into a canal for the passage of the sperm.

The cloaca is large and imperfectly divided. The *proctodaeum* contains the median copulatory organ. The *coprodæum* and *urodæum* are confluent. Into them open the genital ducts, the bladder and the end of the gut. The *urodæum* in some water-tortoises possesses anal sacs (secondary bladder) which are simple diverticulate and function as accessory organs of respiration. The sacs are being constantly filled with water for this purpose. When taken out on land these tortoises suddenly squirt out water. This water comes from these sacs.

period. They are now comparatively reduced in the number of families and genera, but the main divisions that existed in the past occur even today. Six species of *Kachuga* occur in Northern India. Their fossils have been found in the Pleistocene of the Siwalik Hills and Narbada valley.

WHAT IS A SNAKE?

The snakes represent a more modern reptilian group than the lizards. There are a few Cretaceous forms which are possibly primitive snakes, but may be advanced lizards. The snakes have not been found before the EOCENE, and the more evolved snakes appear fairly late in the Tertiary. The snakes are considered late-comers. They are near the peak of evolutionary development today.

The snake is known for its sinuous movement. Its body is elongate and limbless. The most characteristic feature of a snake is to be found in specialization of its skull and jaws, which enable these predatory animals to distend the mouth to an enormous degree and swallow a prey of large size. Some lizards can also widen their jaws and the quadrate is somewhat moveable. In snakes (as in some advanced lizards) the two halves of the lower jaw are connected only by a ligament so that the lower jaws can be spread sideways, and there is, still further a flexible jointed part way back along the lower jaw. Thus in snakes the lower jaws are broken into flexibly jointed pieces so that possible distension is greatly increased. Excepting the brain case everything else in the skull can move. Because of this remarkable flexibility of the whole head skeleton, a snake can distend its mouth to swallow an object much bigger than the diameter of its head, or even of its trunk.

In typical snakes the teeth are curved backward and are arranged in rows on the lower jaws, and above in similar rows on the palatal bones and (primitively) on the jaw margins as well. The prey once seized can never slip forward because of backward curve of teeth, on the other hand, it is gradually pushed back through the mouth and throat into the stomach. It is digested leisurely in the stomach. It is evident, therefore, that the swallowing process is aided by the tooth battery. If a large animal is caught it may be digested in weeks or months, and there is a record of a captive python which went for nearly three years between successive meals.

The body is generally very long and slender usually with two hundred to four hundred segments in the backbone. There are complex joints between the segments facilitating sinuous movement. There are stout curved ribs for attachment of the strong trunk muscles. Some primitive snakes have vestiges of pelvic girdles, and in boas and pythons there is a pair of small claws where the hind legs should be, otherwise all trace of limbs is lost.

Why limbs have been lost in snakes? Some people feel it is easy to move through deep grass if the animal is without limb. Snakes are known to "swim" through deep grass. Another view is that snakes have evolved as swimming eel-like forms. The majority opinion is that ancestral snakes were burrowers. Most of the lizards that have become limbless are burrowers, and most of the living snakes today are burrowers. It is because of burrowing habit that snakes have lost their eye and ear. The eyes are completely sheathed and protected externally by stiff transparent structure formed from the fused upper and lower lids. Snakes have lost their ear drum and appear to have little normal hearing. They are able to detect ground vibrations.

The tongue of snake is very long and slender and deeply forked. It serves as an organ of smell. The tongue when extended picks up from the air tiny smell producing particles and is pulled back. In the roof of the front part of the mouth there are certain pockets that can pick up sensation of smell. When pulled back the forked tips of the tongue are inserted in these pockets and sensation of smell is produced.

There is a greater concentration of snakes in the tropics, their number has diminished in the temperate zones. They appear to withstand cold better than lizard. Temperate zone snakes usually hibernate by gathering en-mass for mutual warmth in a "den" below the frost line. The eggs are generally well covered, and in some cases they

are said to be brooded or guarded during incubation. There is no known instance of the care of the young. Some snakes bear their young alive.

Most snakes adhere closely to a uniform pattern, but there is considerable variation in habits, colouration, and dentition.

Snakes such as the boas and pythons are regarded relatively primitive snakes. Their skull parts are not as freely moveable as in advanced snakes. The term "python" is generally applied to Old World forms, "boa" to the New World forms. There is practically no difference between the two. The presence or absence of a supernumerary bone lying above the orbit is a minor difference between the two. Most boas and pythons are constrictors, they wind their bodies around their prey. The pythons and boas include the largest of snakes.

There are some typical snakes, advanced in skull motility over the boas and pythons, but lacking the specializations (such as tooth reduction) seen in advanced poisonous snakes. There is no popular name for these. They are included in the family Colubridae. They include all the harmless snakes such as the grass snakes, black snakes, racers and so on. Most are of modest size, generally lacking the constricting habit and in majority of forms lacking poison glands. They are not harmful to man, but are useful as destroyers of "vermin". Some tropical species of this family are not harmful to man excepting the South African tree snake.

Then there are the most advanced poisonous snakes. They are highly poisonous and have developed specialized fangs for poison injection. There are three such families. One is almost entirely confined to the tropics of Africa and Asia and has Cobras as its best known members. Cobras are of slender build but their head can be expanded into a hood, which appears to function as a threat or warning. The maxilla bears a small number of teeth, the most anterior one, with which the poison gland is associated, is a fairly good-sized fang fixed in position. It bears along its length a deep groove, which is closed for most of its length to form a tiny injection duct. In the poisonous species of Colubridae the poison is injected along grooves in several teeth of normal size at the back end of the tooth row. These are called "back fanged" snakes.

The cobras and closely related forms have a considerable number of species in Africa and from India eastward to Malaya region. Best known is the Indian Cobra, responsible for a large annual death toll. The giant among poisonous snakes is the king cobra of Siam and adjacent regions, largest of all poisonous snakes, attaining a length of 18 feet.

The Australian snake fauna is a peculiar one. Many of them are small and inoffensive. The largest is the taipan of the north-eastern part of Australia and is said to attack on sight. The tiger snake runs up to six feet, is common and widespread and has an extremely potent venom. The mambas of Africa are highly poisonous arboreal forms, the largest species of which, the large black mamba, is about seventeen feet in length.

The sea-snakes (family Hydrophiidae) are closely related to cobras. The tail and posterior part of the body are flattened from side to side (laterally compressed), forming an effective swimming organ. They are purely marine and in most cases, the young are born alive. They are extremely poisonous but of little danger to man.

A final family of snakes is that of vipers, which include the major poisonous snakes of northern temperate regions as well as a variety of tropical forms. The true vipers include the most familiar of Old World types. A separate subgroup include rattle snakes, copperheads and water moccasins. The poison apparatus is highly developed. The maxilla bears only the very large fang (plus developing replacement for it). The fang is in the form of a moveable sharp-pointed hypodermic needle, the venom passing down its length to the tooth tip in a closed tube. A complicated series of bone articulations form a mechanism by which the fangs are tucked back inside the mouth when the jaws are closed, but erected automatically when the mouth is opened. In contrast to cobra group the vipers typically coil the body when preparing to strike and launch the body straight forward. The vipers have a typically wedge-shaped head, broader behind, separated from the stout body by a narrower neck region. This is in contrast with most other snakes (but some harmless forms have similar contours).

The vipers are widespread in Asia, Africa and Europe and are absent from Australia and the Americas. They are, on the whole, much less dangerous to man than the cobra group.

COMPARISON OF POISONOUS AND NON-POISONOUS SNAKES

I.

Tail is laterally compressed it is sea snake and is poisonous.

II.

Tail is rounded may be poisonous or non-poisonous. Lay the animal on its back and examine the belly scales (ventrals).

A

If the ventrals are broad, extending fully across the belly as in Fig. 6.52 A left below. It may be poisonous or not.

B

If the ventrals are narrow it is non-poisonous (Fig. 6.52 B right above).

Now examine the head

Head covered with scales (Fig. 6.52D, D')—Vipers.

Head covered with shields (Fig. 6.52 C).

Then examine the belly scales

Vipers are poisonous (i) pit viper: a pit (loreal pit) (Fig. 6.52 B) is present between the eye and nostril. These snakes are available in hilly regions. (ii) The little Indian Viper (*Echis carinata*), small snake with loreal pit. An arrow-shaped mark present on the head. Sub-caudals single. (iii) Russell's viper; loreal pit absent: sub-caudal double (Fig. 6.52)

Vertebrae not very enlarged 3rd supralabial (Fig. 6.52 G) touches the nasal shield and the eye—Cobra Poisonous.

Ventrals enlarged only 4 infralabial; the 4th is the largest (Fig. 6.52 E) Sub-caudal single—Krait.

CLASSIFICATION

Reptiles are cold-blooded vertebrates, which breathe by lungs throughout their existence and have the body covered by scales. The skull articulates with the vertebral column by a single median occipital condyle. These basic characters distinguish the reptiles from other vertebrates. The evolution of reptiles was rapid. It is now definitely known that they arose from amphibians and in turn gave rise to birds and mammals. During the secondary or Mesozoic period they were the dominant group of vertebrates and had attained maximum development. By the end of the Triassic most of the orders were established and some became extinct at that time. They are divided into several orders, but only four of these are represented these days

CLASS REPTILIA

Subclass 1. ANAPSIDA

Order 1. *Cotylosauria. Extinct from Carboniferous to Trias.

Examples: *Seymouria, *Captorhinus.

Order 2. Chelonis. Permian to Recent.

Fig. 6.52. Comparison between poisonous and non-poisonous snakes A, ventral scales large (poisonous or non-poisonous snakes); B, Ventral scales of python (non-poisonous snakes); C, head shields; D, head scales of a viper; D', head scales of a pit viper; E, head of Krait Ventral View, F, dorsal scales of Krait; G, head shields of Cobra; H, dorsal scales of Cobra.

Examples: **Varanosaurus*, **Dimetrodon*.

Order 2. *Mesomorphia*. Permian.

Example: **Mesosaurus*.

Order Chelonina Turtles and Tortoises. Body encased between the carapace and the plastron; single nasal opening; quadrate immovable single temporal arcade; usually with an epidermal exoskeleton of horny plates; thoracic vertebrae and ribs firmly fused with the carapace, pectoral and pelvic girdles within the ribs; limbs terminated by claws or paddle-like, teeth absent but the jaws have horny investment.

Sub-order Athecae. Vertebrae and ribs not fused with carapace; skin leathery, without horny plates; parietal bones without descending processes; head not retractile; limbs paddle-like Indian, Atlantic and Pacific Oceans.

Dermochelys, the leathery turtle, has only small bony scales embedded in the skin, has no shell and is over 6 feet long and weighs half a ton.

Sub-order Thecophora. Thoracic vertebrae and ribs immovable united with a series of neural and costal plates, parietals prolonged downwards meeting the pterygoid or separated from them by an epiptygoid.

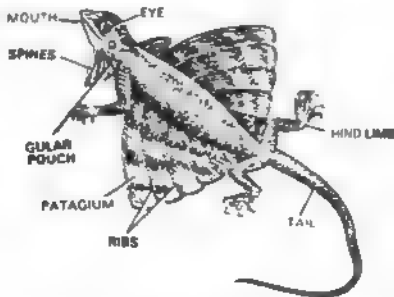


Fig. 6.54. *Draco*.

This includes the terrestrial animals, such as *Testudo graeca*, the Grecian tortoise of South Europe which is herbivorous; the freshwater tortoises such as *Chrysemys*, other American terrapins and *Emys* the European water tortoise.

Chelone mydas, the green or edible turtle, also belongs here. It is over three feet long and prized as food. It breeds in the West Indies, in the Straits of Malacca, and on the coast of West Africa. They are caught as they come ashore and made into turtle soup.

Trionyx is a fresh water turtle with neither bony nor horny scales. *Trionyx gangeticus* is a common species found in the local rivers.

Order 2. Rhynchocephalia. Lizard-like reptiles with vertebrae amphicoelous; quadrate immovable; upper and lower temporal arcades present, acrodont teeth; premaxillae resembling incisors of rodents; mandibular symphysis ligamentous; skin with horny scales; vertebrae contain persistent remains of notochord; ribs single-headed and with uncinate processes.

In common with the many extinct species *Sphenodon* shows many primitive reptilian features. It has no copulatory organs. It was once widespread throughout New Zealand, but became much reduced and is in danger of extinction. Strong conservation measures have now allowed it to grow in numbers and it is confined to small islands in the Bay of Plenty.

Sphenodon evidently is a type related to extinct reptiles of remote times, yet its habits and soft parts are like those of lizards. For this reason it is often called a "living fossil."

Order 3. Squamata. Lizards and snakes. Skin with horny epidermal scales or shields; quadrate bone movable; vertebrae usually procoelous, copulatory organs (hemipenes) double and eversible.

Sub-order **Lacertilia (Sauria)**. Lizards. Reptiles with horny epidermal scales; movable quadrate bones; transverse anal opening; a cloacal bladder and two sacral vertebrae. The two rami of mandible are firmly connected at the symphysis; eyes with movable eyelids and nictitating membrane; tympanic cavity present.

The sub-order contains twenty six (6 fossil) families. Only a few specialised and interesting forms are described below.

Hemidactylus (family **Gekkonidae**) are small lizards with digits free or partly webbed, more or less strongly dilated with a double series of lamellae beneath. Dorsal scales granular, uniform intermixed with large tubercles in oriental species. Pupil vertical. Males with preanal and (or) femoral pores. Tongue protrusible. Many produce sounds. Egg-shell calcified. World-wide in distribution. *Gekko gekko*, the wall lizard, is another example of the family.

Phrynosoma (family **Iguanidae**), the horned toad, with spikes on the head and back, is found in the Western American deserts and has the habit of burrowing in the sand. This is the only iguanid in which the eggs develop within the mother.

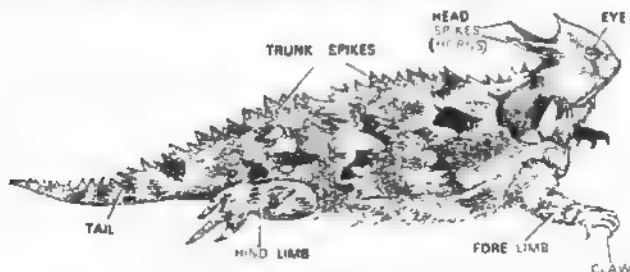


Fig. 6.55. *Phrynosoma*.

Draco (family **Agamidae**), the Flying Dragon. Ribs much prolonged supporting a lateral wing-like dermal expansion on each side, by means of which the animal is able to glide among trees. **Osteoderms** (bony plate) absent. Tympanum distinct or covered with scales. No femoral or preanal pores. The flying lizards are entirely arboreal in habits, seldom descending voluntarily to the ground. They feed upon insects, etc. In many species the wing membranes are adorned with colours. The young are produced from eggs, from two to five being laid at a time. About 40 species of *Draco* are known from Indo-Chinese region, the East Indian Archipelago and the Philippine Islands. One species is found in Southern India (Fig. 6.55).

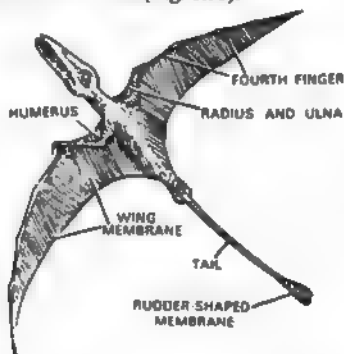


Fig. 6.56. *Pterosaur*, restoration of extinct flying reptile

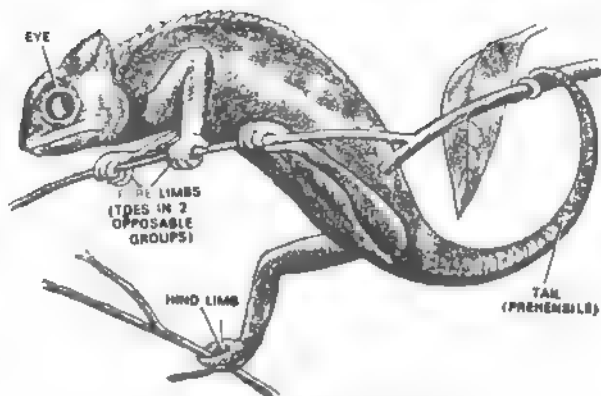


Fig. 6.57. Chameleon—the lizard that changes its colour

Crotaphytus collaris (family Agamidae) is the collared lizard of about 13 inches length; sexes differ in coloration, lives in rocks and open ground. *Agama*, *Uromastix* and many others of this family are found in India and other places.

Chameleon (family Chamaeleontidae). Tongue protractile to a length equal to that of the body, club-shaped and viscose, digits arranged in two bundles of two and three; eyes large and covered with a thick granular lid pierced by a small central opening for the pupil; tympanum and tympanic cavity absent, parietal single, forming a knob-like crest; tail prehensile, coiling ventralwards. These animals undergo remarkable changes of colour. Africa, Madagascar, India and Ceylon

Heloderma (family Helodermatidae). Gila monster This is the only poisonous lizard. Body elongated and covered with ugly tubercles; limbs short, well-developed and powerful, tail thick with reserve fat; teeth fang-like and grooved with labial

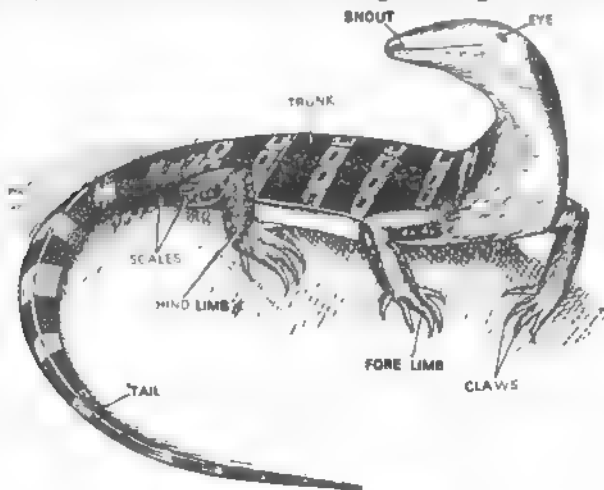


Fig. 6.58. Varanus—the monitor lizard.

poison-glands; osteoderms present. Found in Mexico.

Ophisaurus (family Anguidae) Body elongated and snake-like, limbs absent but limb-girdles present, osteodermal plates present on the head and body; eyes with movable lids. These limbless lizards live on slugs eating also earthworms and snails. They can be distinguished from snakes by the presence of movable eyelids and the tympanum (which are absent in snakes). Further, in snakes the mouth can be very widely opened because of the free articulation of the lower jaw which is not the case with snake-like lizards. They are viviparous producing young which differ in colour from the adults. The adults are light or dark brown above (*O. gracilis*), with darker lateral band and frequently irregular transverse series of blue, black-edged spots. The young are light brown (or whitish) above, with small blackspots and a very dark brown band extending along the side of the head to the nostril and along the side of the tail.

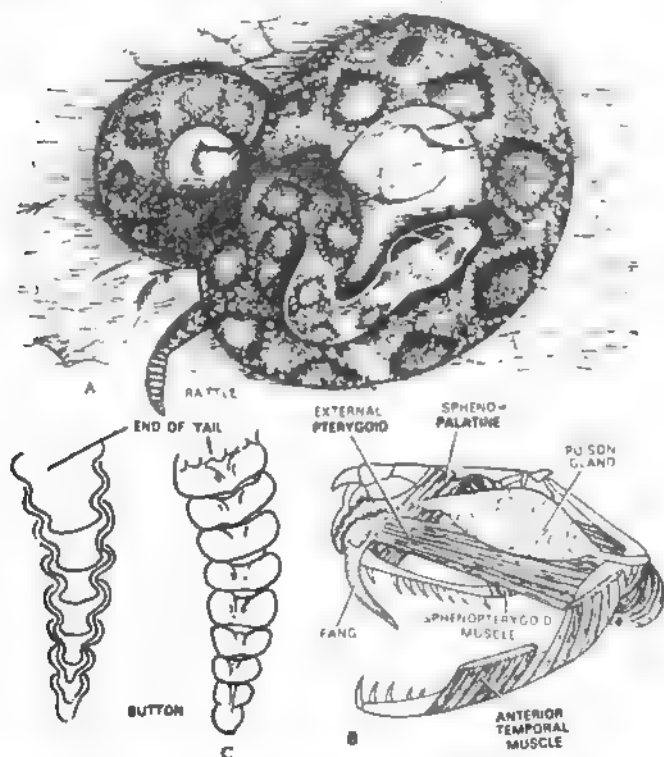


Fig. 6.59. *Crotalus* sp. - the rattlesnake. A, the entire animal. B, dissection of head showing poison gland, C, the rattle; D, longitudinal section of the rattle.

The Burmese glass-snake, as it is called, is common in many parts of Eastern Himalayas, Assam and Upper Burma (Darjeeling district) at between 3,000 and 5,000 feet altitude.

Anguis fragilis, the slow worm, is another limbless lizard, *Amphisbaenas* have also lost the limbs and live a worm-like life completely underground.

Lacerta (family Lacertidae) are the old world lizards in which limbs are normal,

post-temporal fossa roofed and the intermaxillary are unpaired. Found in Europe, Asia and Africa.

Varanus (family **Varanidae**). Monitors are large lizards with short trunk and limbs and long neck and tail. Scales small, smooth; teeth large pointed and pleurodont. Tongue long smooth deeply bifid and protrusible. About thirty species are known. All are confined to the old world being found in warm parts of southern Asia, Africa, the East Indies, and the Australian region. All of them are carnivorous and are usually prepared to eat animal food of any kind that they can overcome.

Sub-order Ophidia. The snakes are elongated reptiles without limbs and limb girdles with the exception of a rudiment of a pelvic girdle in some, e.g., *Pythons*. Horny epidermal scales without osteoderms. The mouth is very extensible and even the upper jaw can move relative to the cranium — quadrate bones are movable. The middle ear apparatus is lacking. The tongue is sensory. Some snakes have poison fangs. The vertebrae are procoelous and bear extra-articulating facets. The lower border of both temporal vacuities has vanished. The anal opening is transverse. Without eyelids, urinary bladder and sacrum. The rami of the mandibles are united at the symphysis by an elastic ligament.

About 400 genera and 1,800 species are known. Very few fossil forms are known.

Bor (family **Boidae**), the pythons. Usually large snakes in which the maxillary and mandibular teeth gradually decrease. The nostrils are placed between two or three nasals and these are separated from those of the other side by small scales. Eyes are functional and free, the pupil is vertical. Vestiges of hind limbs and pelvis are present. The tail is short and prehensile. Prefer wooded districts, climbing trees, crush their prey in the coils of the body. World-wide in distribution except New Zealand.

Vipera russeli, Russell's viper, (family **Viperidae**). Nine genera and about forty species of the vipers are known. Of these Russell's viper is one of the scourges of India.

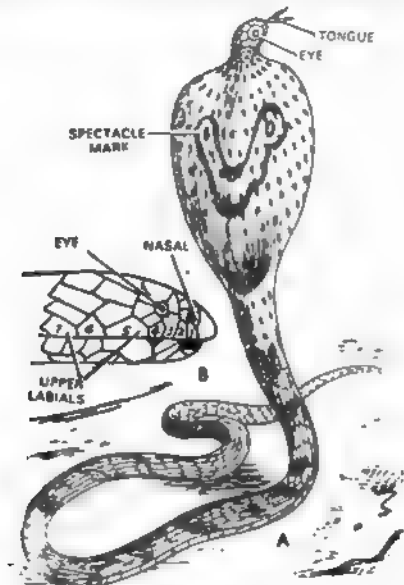


Fig. 5.60. *Naja* sp. A, the cobra, an old world venomous snake; B, side view of the head showing arrangement of scales.

Burma and Ceylon. The upper surface of the body is covered with small, imbricating, usually keeled scales. The general colour is pale brown above with three longitudinal series of black, light-edged rings, often encircling reddish spots. The under surface is yellowish white uniform, or with small crescentic black spots. Usual length is five feet.

Crotalus (family *Crotalinae*), the Rattle-snakes. These have a deep cavity or pit between the eye and the nose, lodged into the hollowed out maxillary bone hence also called "Pit-vipers." *Crotalus* has got a rattle at the end of the tail. The rattle is composed of a number of horny bells which fit into each other. The terminal bell is in reality the horny covering of the tail. Now and then some of the bells break off, probably when worn out, and a new set gradually replaces them. As the snake moves the rattle produces strange rattling noise, a shrill sound like that of a rattling alarmclock. The upper surface of the head is covered with small scales. The supra-ocular shields are broader often transversely striated. The largest of rattle-snakes attains a size of 8 feet.

Enhydryna (family *Hydrophinae*). Sea-snakes. The characteristic feature of the sea-snakes is that the tail is strongly compressed. All the scales are small, often the ventrals are not enlarged. Eyes are small with round pupils. All the sea-snakes are very poisonous and live in the sea with the exception of one species of *Disterna*, which is found in a fresh water lake in the Philippines. They live on fish. In *Enhydryna* the maxillaries carry two or more small grooved teeth besides the poison fangs. The back is olive or dark-grey with black transverse bands. The under surface is white. The species is found in the Indian ocean.

Naja (family *Colubrinae*) belongs to sub-family *Elapinae* which comprises about 150 species. The tail is cylindrical, the pair of large grooved poison-fangs are separated by the interspace having from one to three small, faintly grooved teeth near the posterior end of the maxillaries. The scales are smooth and without pits, and are arranged into fifteen to twenty-five oblique rows on the trunk, though more occur in the region of the neck. The head is slightly distinct from the neck. Each nostril lies between two nasals and the internasal. The pupil is round. The neck region can be expanded into a hood as the ribs of the region spread and move headwards. Several species of *Naja* are known. The cobra is *N. tripudians*. A black and white speckled mark on the dorsal side of the hood is a characteristic feature of its coloration. The cobra is widely distributed and ascend to 8,000 feet above sea level in the Himalayas. Large specimens may attain six-feet length. The cobra prefers places which afford it a convenient hole to retire into, for instance, deserted hills of termites and ruins etc. It makes itself at home in inhabited houses especially in villages.

Order 4. Crocodilia. Tail long and with a dentated dorsal crest, paired in front, but single behind, fore-limbs with five digits, hind limbs with four webbed digits; nostrils at the tip of the long snout, can be closed, false palate present, back and belly with transverse rows of bony plates which are overlapped by epidermal plates, the plates of the back are pitted, sculptured or keeled; abdominal ribs and nictitating membrane present; teeth lodged in sockets, pubis excluded from acetabulum; long prepubis

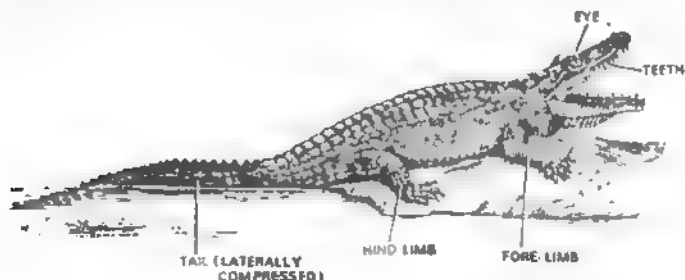


Fig. 661. Alligator sp.—a carnivorous reptile of United States and China.

present; quadrate immovable. Heart with a completely partitioned ventricle, and two aortic arches. Lungs well developed, lodged in a cavity separated from the abdominal cavity by a transverse partition (not itself muscular).

The two living families of the order are *Gavialidae* and *Crocodylidae*.

Gavialis (family *Gavialidae*). Snout: long (hence called longnosed crocodiles) and slender, nasals widely separate from nasal aperture. They are fish eaters. India, Burma and East Indies.

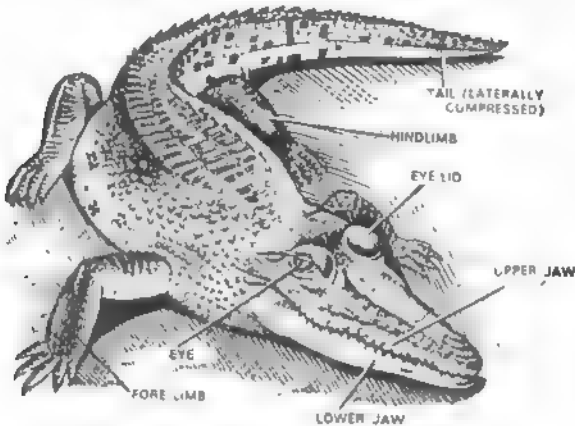


Fig. 6.62. *Crocodylus* sp.

Crocodylus (family *Crocodylidae*). Head long; teeth unequal; large horny scales reinforced by thick dermal bony plates especially on the back; without bony nasal septum and ventral armour. It is most widely spread genus occurring in Africa, South Asia, North Australia and tropical America.

Alligator. Head short and broad; teeth very unequal; fourth mandibular tooth fits into a pit in the upper jaw; with a bony nasal septum and with ventral scutes. China and North America.

Caiman. Without bony nasal septum; dorsal and ventral armour articulated together. Rest as in *Alligator*. Central and South America.

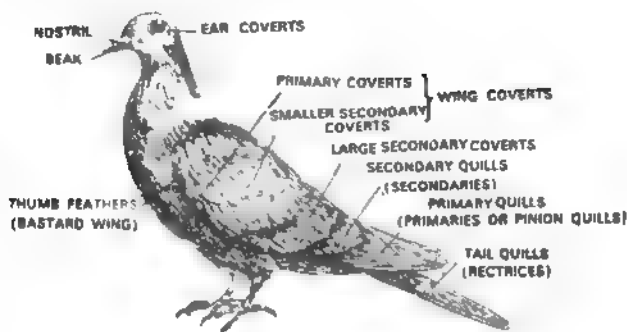


Fig. 7.1. External features of pigeon.

EXTERNAL CHARACTERS

The body of a bird is divided into many regions such as the head, the neck, trunk and tail. The head (Fig. 7.1) is elongated anteroposteriorly with its rounded cranium and prominent beak formed by the upper and lower jaws covered by horny sheets. At the base of the beak is a small patch of skin, the **operculum**. The head bears two large eyes provided with the upper and lower eye lids and a semi-transparent **nictitating membrane**. The neck is long cylindrical and very mobile sharply marked out from the head and the trunk. The trunk is plump and somewhat compressed from side to side. The boat-shaped **carina** or keel of the sternum is raised into a prominent ridge along the midventral line. Posteriorly the trunk is drawn out into a short conical projection, the **true tail** or **uropygium**, from which originates a group of large feathers, to which the term "tail" is generally applied.

The trunk bears a pair of wings which correspond to the forelimb of any other terrestrial vertebrate and two walking legs corresponding to the hind-limbs. The wings show three typical divisions of the fore-limbs, the **upper arm**, **fore-arm** and the **hand**. The parts of the hand are closely bound together by skin. The several bones can be indentified by feeling them through the skin. Between the upper arm and the fore-arm, on the anterior side extends fold of skin the **alar membrane** or **prepatagium**. A similar fold exists between the posterior portion of the upper-arm and the trunk, this is the **post-patagium**. The hind-limb has a short **thigh** closely bound to the trunk, a long **shank** extending from the knee downwards and backwards and a foot clearly divisible into a proximal portion, the **tarso-metatarses** and four **digits**.

The **mouth** is terminal guarded by the upper and lower jaws covered by horny beak. It has a wide gap. Between the beak and operculum there is a pair of slitlike apertures, the **nostrils** that lead into the olfactory chamber. Below and slightly behind the posterior (or outer) angles of the eye are two circular openings, the **external auditory apertures**. Towards the posterior end of the body there is a large transverse slit situated ventrally at the junction of the uropygium and the trunk. This is the **cloacal aperture**.

The skin of the pigeon (like most birds) is loose and thin. It is made up of usual two layers, the **epidermis** and **dermis**, both of which are reduced to a delicate thinness. Those parts that are not covered by feathers like the shanks and, areas around the base of the beak, exhibit a thickened corneal layer of epidermis. The looseness of the skin has a definite advantage, it enables the muscles of flight to move freely. The characteristic feature of the skin is the possession of feathers. Other exoskeletal structures of the avian skin include beaks, leg-scales and claws, all of which are entirely epidermal in nature (dermal elements like scales of fishes or the bony plates of certain reptiles are absent in birds).

Feather Excepting the lower joints of the legs and the toes nearly the whole surface

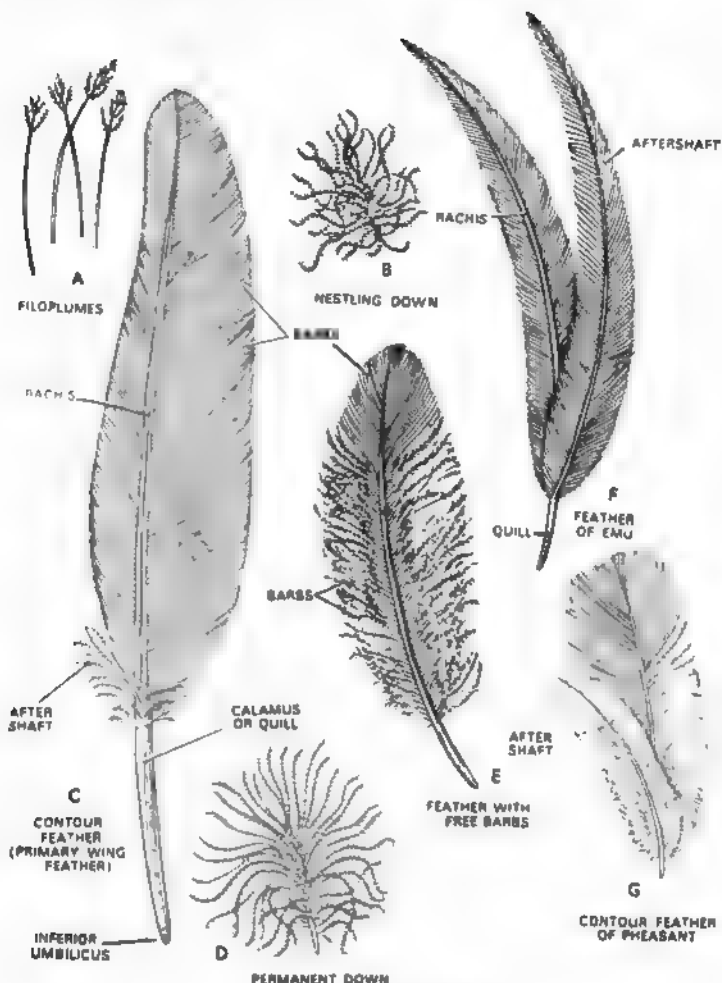


Fig. 7.3. Various kinds of feathers.

like elevation on the surface of the skin. This is the **feather-germ** and grows outward as a tapering epidermal cylinder fitted with mesodermal core. As the feather-germ elongates a pit, the **feather-follicle**, develops round its base. The germinative layer of each epidermal thickening gives rise to an **intermediate layer** of cells between itself and the stratum corneum. Later on two adjacent longitudinal ridges appear on the inner surface of the distal third of the feather germ. These elongate and extend over the full length of the germ. They are the **barb-ridges**. Additional barb-ridges appear rapidly in sequence to the right and left of the original pair until ten or eleven longitudinal ridges are formed, spread over the entire circumference. The

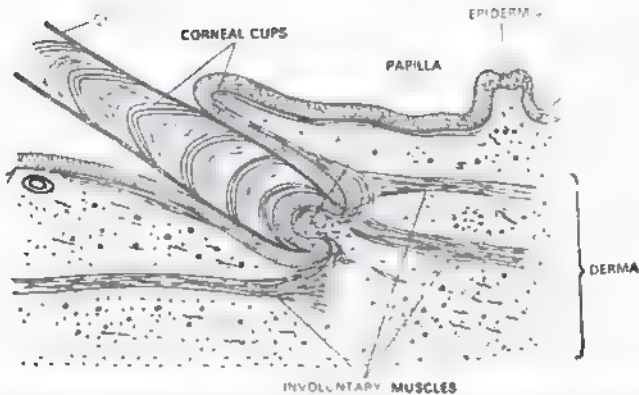


Fig. 7.4. Development of feather of pigeon. The corneal cups are left due to periodical withdrawal of the papilla (after Krause).

barb-ridges are formed entirely from the intermediate layer of epidermal cells clothed internally by a layer of "cylinder-cells" (the former germinative layer) and covered externally by a smooth sheath of flattened cells (made of the stratum corneum). Additional ridges may be produced in between the original ridges or by splitting off from one of the previous ridges till the number is fifteen or thereabout. The ridges elongate towards the base of the feather germ. On either side of the base of each

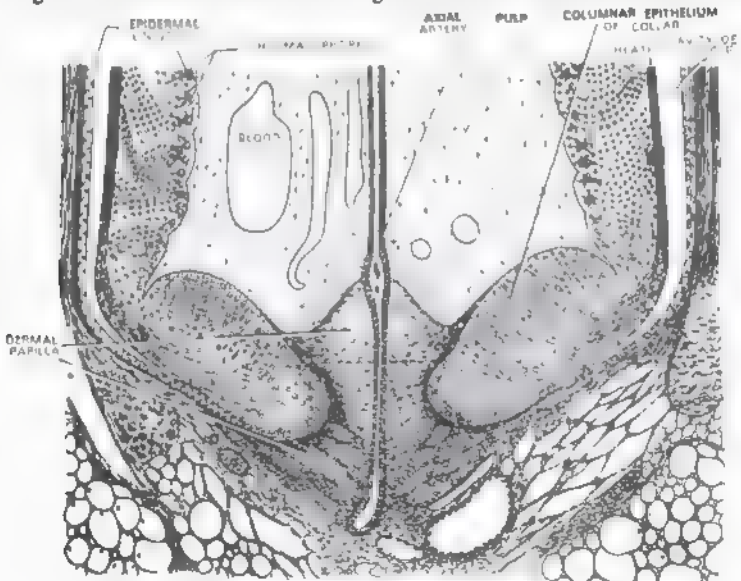


Fig. 7.5. Details of the basal portion of a regenerating feather in longitudinal section (after Lillic and Wang, '41).

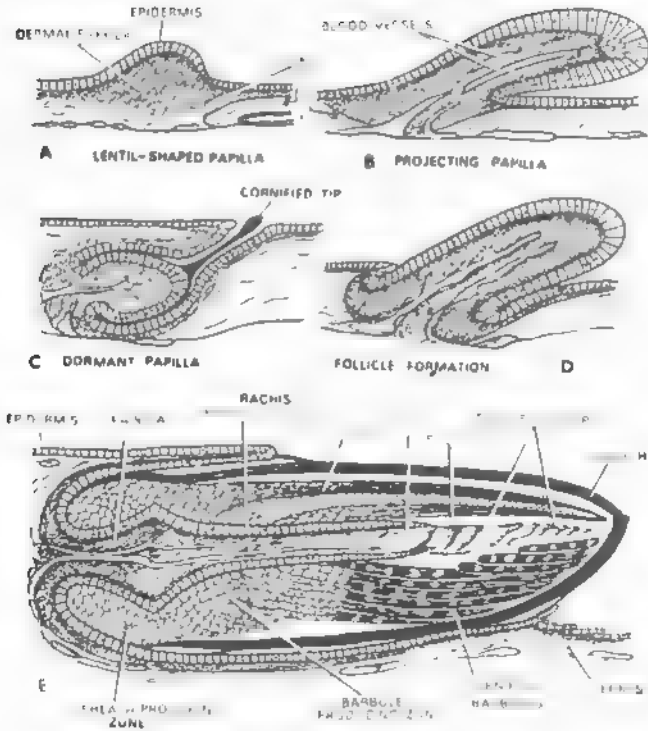


Fig. 7.6. Development of contour feather

At the same time the bases of the other barb-ridges become tilted towards the dorsal side of the cylinder so that further growth of these ridges causes them to bend tangentially towards the forming rachis.

The growth of the feather becomes rapid with the appearance of rachis. As the collar adds to the length of the feather the bases of new barb-ridges are prolonged tangentially until they become rooted in the formative zone of the rachis. Their modified bases form the lateral portion of the shaft. The vane of the feather is thus formed by the addition of the consecutive series of barbs to the progressively elongating rachis. It follows from the mode of origin that the oldest part of rachis is the tip of the feather, and the oldest part of the barbs is at the margin of the vane. The barbules are formed as in the down feathers (Fig. 7.6C).

Types of Feather. The quill feather (Fig. 7.3C) are the largest feathers of the bird. The wing quills are known as **remiges** and the tail quills are **rectrices**. The remiges or wing quills have inner or posterior half of the vane much broader than the outer or anterior half. The wing feathers are divided into **primaries**, **secondaries** and **tertiaries**. The **primary quills** are those that are attached to the bones of the manus. In all there are eleven primaries (Fig. 7.8) and are known according to their position. Six feathers attached to the middle metacarpal are called **metacarpal quills**, one attached to the phalanx of the post-axial digit is called **ad-digital**, and two attached to the distal phalanx of the middle digit are known as **mid-digital** and two attached to the distal phalanx of the middle digit are called **pre-digital** quills. One of the predigital quills is

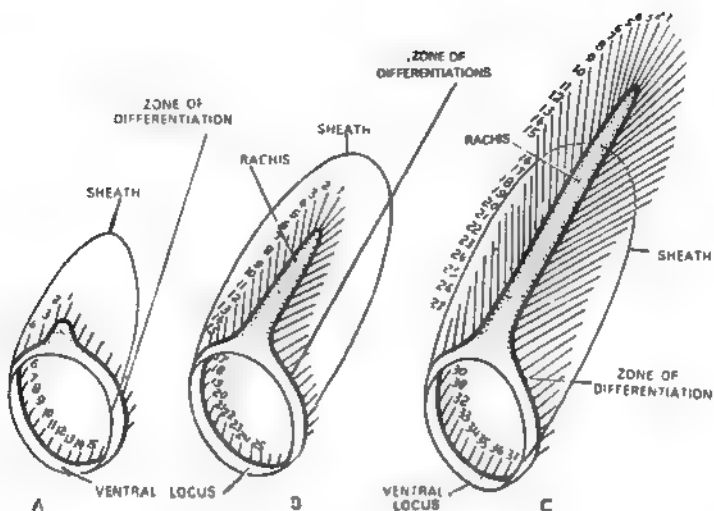


Fig. 7.7. Three stages in the development and elongation of rachis. A., the rachis is forming and there are 15 barb-ridges of the first complement, thereafter (B and C) new barb-ridges arise serially on each side of the ventral locus, become oriented tangentially with their bases slanted toward the rachis. Finally barb-bases shift toward the rachis and meet it forming two halves of the vane

smaller. The quills that are attached to the ulna are known as **secondary quills**. The **tertiaries** are attached to the humerus and elbow. The **rectrices** or tail feathers are twelve and have the two sides of the vane almost equal in size. Smaller quill feathers are called **coverts**. They cover bases of the quill feathers of the tail and the wings.

The **down feathers** are short, and woolly feathers, without shaft, forming a general

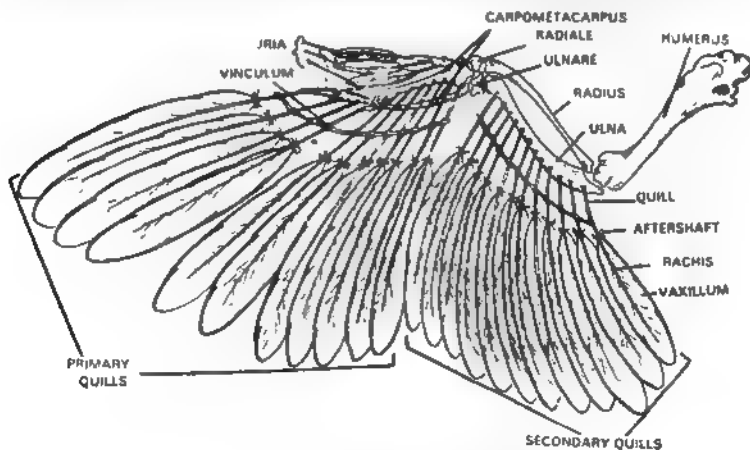


Fig. 7.8. Attachment of the wing feathers.

other methods for heat-regulation. In many birds a conical elevation is present immediately in front of the tail. This is the **oil gland (uropygium)** or **preen gland**. Formerly it was believed that the secretion of this gland was used to water-proof the feathers. But now it has been found out that there is no trace of oil on feathers and it is not used for water-proofing. The oil is used to keep the covering of the beak in good condition while the beak is used for trimming the feathers or preening. Some experiments demonstrate quite conclusively that secretions from the oil gland help keep the feathers in good condition and serve as water-repellant. Thus, the exact function of the oil gland seems uncertain. In the pigeons there is no oil gland.

ENDOSKELETON

The skeleton of a bird is, in general plan, the same as that of other vertebrate animals. One of the chief characteristics of the birds' bones is their lightness, an adaptation to flight. The birds may have large bones but they are not compact. Many bones have great cavities with no marrow, some of which may contain prolongations of the air-sacs. The bone, correctly speaking, is solid round the walls with a mass of spongy network within. Essentially the endoskeleton consists of a strong cranium made of many bony elements, which is attached to a strongly articulating compact vertebral column. To this axis (axial skeleton) are attached the various appendages.

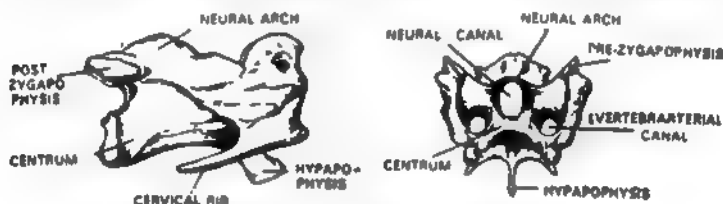


Fig. 7.10 Structure of cervical vertebra. Left, lateral view and right, posterior view

Vertebral Column. The number of vertebrae in birds is most variable. There are three characteristics of vertebral column of a bird (i) the neck is long, being equal in length to the remaining length of the column, (ii) the trunk region is rigid because the thoracic vertebrae are fused, (iii) the shortness of the tail, the number of vertebrae itself is short while the posterior ones fuse to form the pygostyle. The vertebral column is divisible into regions, i.e. **cervical, thoracic, lumbar, sacral and caudal**. The cervical vertebrae are the vertebrae of the neck region. In the birds it is difficult to distinguish between the thoracic and the cervical vertebrae. The usual practice is to regard the first vertebra having its ribs articulating with the sternum as the first thoracic vertebra; all those anterior to it are the cervicals. A typical cervical vertebra is a long one as compared to the vertebra of *Varanus*. Its **centrum** (Fig. 7.10) is slender having saddle-shaped surfaces, the anterior one being concave from side to side and convex from above downwards while the posterior face is convex from side to side concave from above downwards. The **neural arch** is shorter than the centrum and is notched in the middle line both anteriorly and posteriorly, the neural spine is rudimentary. The **transverse processes** are fused with the cervical ribs forming a sharp backwardly directed process having a foramen at its base. Through the foramen passes the vertebral artery hence it is called **vertebrarerial canal**. The **zygapophyses** or the articular facets are in two sets. The **pre-zygapophyses** are flat articular facets on the anterior side, facing upwards and inwards. The **post-zygapophyses** are the posterior articular facets projecting backwards from the posterior border of the neural arch and facing downwards.

The first two vertebrae are specially modified, the first to receive the skull and the second to articulate movably with the first. Of these the atlas or the first cervical vertebra is a light bony ring just like that of *Varanus*. Its ventral portion is thickened

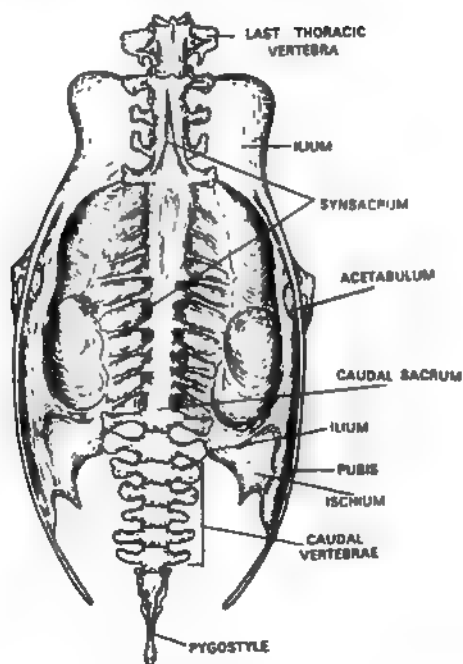


Fig. 7.13. Synsacrum of pigeon.

in number. The centra of the anterior ones among these are laterally compressed and in the hind-most two or three the centra are dorso-ventrally compressed. The transverse processes, except in the last, are double, that is, made up of two elements. The dorsal elements of these fuse to form bony plates continuous with those of the vertebrae in front. The ventral elements of the transverse processes are rod-like in the case of the first four or five vertebrae and are regarded as ribs, as they ossify independently of the centra. In the hinder vertebrae they are smaller. Between the bodies of these vertebrae and the ilia are deep hollows, which lodge lobes of the kidneys. All these vertebrae are fused to form the compound synsacrum. The bones of the synsacrum are so intimately fused that it becomes difficult to distinguish them clearly. (d) The caudal region is short consisting of six to seven movable vertebrae of which the last consists of a vertical, laterally compressed plate, the **pygostyle** or **ploughshare**, formed by the fusion of four or more of the hinder most caudal vertebrae (Fig. 7.14). It is this part that supports the rectrices.



Fig. 7.14. The caudal vertebrae of fowl.

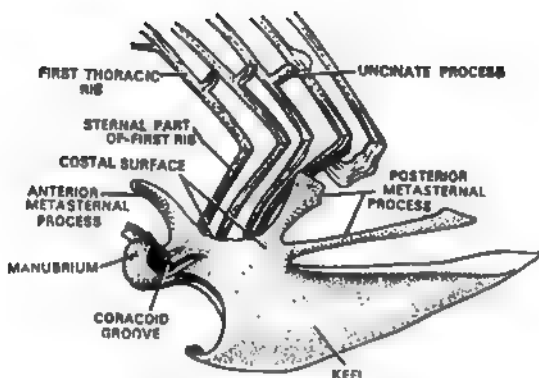


Fig. 7.15. Ribs and sternum of fowl.

Ribs and Sternum. There are two types of ribs in birds, the **cervical** and **thoracic** and there is a massive **sternum** provided with a prominent **keel** to accommodate large muscles of flight. The **cervical ribs** are the two movably articulated ribs, as noted above. The first is small but has distinct capitular and tubercular articulations; and the second is larger and on its posterior border bears a backwardly projecting **uncinate process** (see below), which overlaps the next rib. The **thoracic ribs** are five flattened bony rods attached to the thoracic vertebrae by two processes (a) the **capitulum** attached to the centrum, and (b) the **tuberculum** to the transverse process or the neural

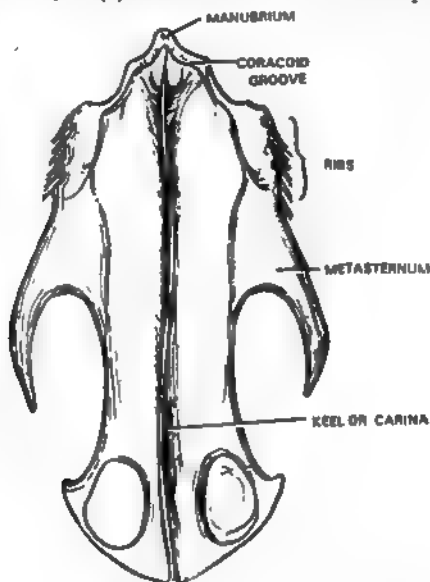


Fig. 7.16. Sternum and keel of pigeon, ventral view

stout straight bone directed ventralwards and is articulated with the coracoid groove on the antero-lateral edge of the sternum. On the outer side it bears a cup-shaped depression completing the **glenoid cavity**. The coracoid is also produced into a process directed upwards and inwards. The **clavicle** is attached to this process. Thus, a foramen, the **foramen triosseum** (Fig. 7 23), is left between the three bones, through which passes the tendon of the subclavius for insertion into the back of the humerus. The **clavicles** are a pair of slender curved bones connected by their expanded upper ends with coracoid and scapula, as mentioned above. Ventrally the two clavicles fuse forming a laterally compressed rounded plate. The bone thus formed is the "**merry thought**" bone or the **furcula**.

The **fore-limb** forms the skeleton of the wing and presents the structure of a typical pentadactyle limb. The bone articulating with the girdle is the **humerus**, and is elongate bone expanded at both the ends. The **head** is expanded and fits into the glenoid cavity. The head is bordered by **preaxial** and **postaxial tuberosities**. From the preaxial tuberosity extends a short **deltoid ridge**. The postaxial tuberosity is large and has a **pneumatic foramen** close to it on the proper dorsal face of the proximal end (Fig. 7 23). Distally the trochlear end of the humerus articulates with the bones of the fore-arm.

The **fore-arm** consists of two bones the **radius** and the **ulna**. The radius is a slender bone articulating with the **trochlea** of the humerus proximally and the carpus distally. The **ulna** is stouter than the **radius** and is also larger. A small **olecranon process** projects from its proximal end beyond its articular facet for the trochlear end of the humerus. Distally it articulates with the carpus. The carpus consists of only two bones in the adult (in the young birds the distal carpal row consists of three pieces which later fuse with the metacarpus). Of these the **ulnare** articulating with the ulna is the larger, whereas the **radiale** is smaller. The manus in the adult consists of a **carpometa-carpus** formed by the fusion of metacarpals with the distal row of carpals. It consists of two rows, the proximal of which is the stronger of the two, and more or less, straight. This represents the second metacarpal with the base of which is fused the first metacarpal. With the first metacarpal articulates a single-pointed phalanx of the first digit. Distally the stout rod bears two prominent phalanges of the second digit. The third metacarpal is represented by the thinner, slightly curved rod on the postaxial side and carries a single-pointed phalanx of the third digit.

The **pelvic girdle** again presents the typical triradiate structure. The ilium, ischium and pubis, the three common components of the pelvic girdle are present in this case also, though in an entirely different form. All the elements of each side are perfectly fused with the **synsacrum** in between forming a more or less shield-shaped structure covering the organs of the body cavity from above. As usual the **acetabulum**, for the articulation of the femur, is present at the junction of the three bones. Each half of the girdle consists of the following parts (Fig. 7 24). The **ilium** is a remarkably expanded bone extending both anterior to the acetabulum and also posterior to it. The inner border of the ilium is fused with the **synsacrum**, whereas, the outer surface of its anterior part is concave. Posteriorly it is fused with the **ischium**. On the outer surface, above the acetabulum, is a projection the **antitrochanter** that articulates with the **great trochanter** of the femur. The **ischium** is directed backwards parallel to the hinder part of the ilium to which it is attached posteriorly enclosing, just behind the acetabulum, an oval **iliosciatic foramen**. The **pubis** is a slender bone directed backwards parallel to the outer and ventral margin of the ischium, with which it is often fused. Behind the acetabulum the pubis and ischium are separated by a slit-like opening, the **obturator foramen**. The acetabulum is formed by all the three bones and is perforated. It is a rimmed cup-like depression for the articulation of the head of femur.

Like the fore limbs the **hind-limbs** also present the typical pentadactyle structure. The bone that articulates with the pelvic girdles is the **femur** or **thigh bone**. It is a short and powerful bone enlarged at both ends. The rounded head is proximal, on the outer (postaxial) side of which is an irregular process, the **great trochanter**. Distally the femur presents in front a deeply grooved surface for the **patella**, which is a sesamoid bone forming the knee joint. The leg or **crus** consists of a **tibiotarsus** and **fibula**. The **tibiotarsus** is a long bone forming the crus. It is chiefly composed of a tibia fused with

breeding plumes in sexual displays, and providing for the many complicated movements of the wing and tail feathers in flight. These muscles have not been critically studied in most species. The Canada goose, for instance, is reported to have about 12,000 individual muscles in the skin for performing such feather-moving functions. These muscles are named in groups corresponding to the feather tracts to which they are distributed. As such the cutaneous muscles of the feathers of humeral tract may be called **humeral cutaneous muscles**, and so on.

The jaw musculature is modified in response to feeding habits. In birds of prey, and seed-eaters (which actually crush seeds) the **adductor** muscles which close the jaws are strongly developed, whereas in insectivores, or in birds that merely pick up and swallow seeds (pigeons) they are generally reduced. The adductor muscles are known as **adductor mandibulae** and are arranged in four sets. Likewise the gaping muscles or **protractors** also show modifications. The protractors mainly include **depressor mandibulae** muscles which are less massive in the seed eaters, but strongly developed in those fruit eaters that puncture fruit with a closed bill and then open it to extract pulp

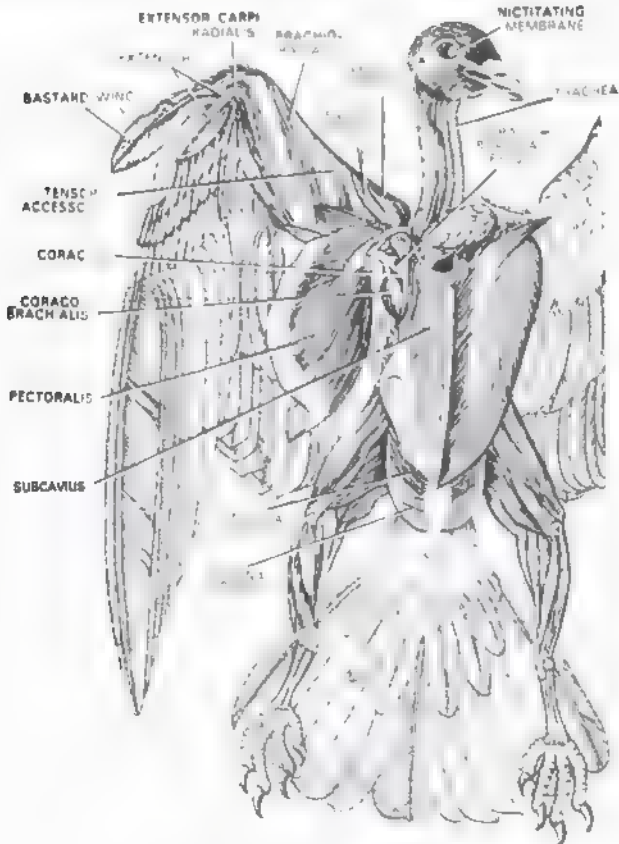


Fig. 7.25. Flight muscles of pigeon

or juice. The meadowlarks, for example, have well-developed protractors and the common grackle has well-developed adductors.

Flight Muscles. The flight muscles on the breast of a bird are large and better known. These consist of one depressor, one elevator, two accessory depressors and four tensor muscles. The largest and the most superficial of these is the **pectoral** muscle (also called **pectoralis major**). This enormous triangular muscle occupies the whole space of the ventral half of the keel of the sternum. Its broad flat tendon is inserted on the ventrolateral surface of the humerus. It is the great depressor muscle, i.e., it pulls the wing to the lower side. For elevating the wing there is another smaller **subclavius** muscle (also called **deep pectoral** or **pectoralis minor**). This also originates on the sternum beneath the **pectoralis major**, and inserts on the dorso-medial aspect of the humerus. Insertion of the subclavius on the upper surface of the arm bone is achieved by the passage of its long narrow tendon through the **foramen trisosseum**. It is the only muscle that elevates the wing. The origin and attachment of the subclavius is just like that of the pectoral yet they function differently because after passing through the foramen trisosseum the tendon of subclavius turns round to be inserted on the dorsal surface and reverses the action of the muscle.

Among the accessory depressors are the **coraco-brachialis longus** and **coracobrachialis brevis**. The longus appears as triangular muscle immediately on cleaning the pectoral and the subclavius. It arises from the posterior two-third portion of the coracoid and from the costal process of the sternum. Its narrow tendon is inserted on the post-axial aspect of the head of the humerus. The coracobrachialis brevis is a narrower muscle in front of the coracobrachialis longus. It arises from the middle of the antero-dorsal aspect of the sternum just in between the junction of the two coracoids. The coracobrachialis brevis muscles of both the sides arise from the same spot and take opposite courses. In some pigeons that are especially kept for flight this muscle shows two divisions, one going to the dorsal aspect, as described and the other turning round the corner internal to the foramen trisosseum to be attached to the anterior aspect of humerus.

Then there are some muscles that keep the wing fully spread (tense) during flight. These are the **tensor muscles**. The longest among these is the **tensor longus**. It rises from the anterior aspect of carpometacarpus, runs along the outer border of prepatagium and is inserted on the front of the head of the humerus. It is a very delicate muscle, and thus, it often becomes difficult to see it. It keeps the outer border of prepatagium fully stretched. A thin sheet of muscles, the **tensor brevis**, spreads between the biceps muscles and the posterior margin of the proximal portion of the tensor longus. Lying across the prepatagium there is a comparatively broader muscle, the **tensor accessorius**. All these muscles keep the prepatagium fully stretched. A thin strip of muscle, the **tensor posterius**, runs along the outer edge of the postpatagium and keeps it fully stretched during flight.

Leg Muscles. The movements of a bird are restricted, there being no movements of abduction and adduction, which a man makes at the hip during walking. These movements are replaced by movements of rotation at the knee. It will be seen that a bird is "sitting down" while it is standing up since the knees are directed forward horizontally. When a bird perches (squats on a perch) the leg bones jack-knife together, thus pulling the tendons attached to the toes so that the phalanges clinch around the perch. This pulling of the tendon is brought about by the body weight, as such to unlock the foot the body has to be raised.

Muscles of Thigh. The muscles around the hipjoint form a system of couples (or braces) that help in balancing and locomotion. The **lateral** and **medial** (**abductor** and **adductor**) muscles are very poorly developed (Fig. 7.26). The **anterior** muscle (**protractors**) are well developed and include the following: (i) the **sartorius** (**iliotibialis internus**), a prominent muscle running from the ilium to the tibia (Fig. 7.26), (ii) the **ilio-tibial**, a large muscle inserted through the patella on a ridge on the front on the tibia thus crossing both hip and knee joint and (iii) the **femorotibial** muscles, associated with ilio-tibial forming the extensor system of the knee. The lateral side of the hipjoint has rather small muscles including the **ilio-trochanteric** muscles that are small braces acting mainly as medial rotators and the **ischio-femoral** and **obturator**

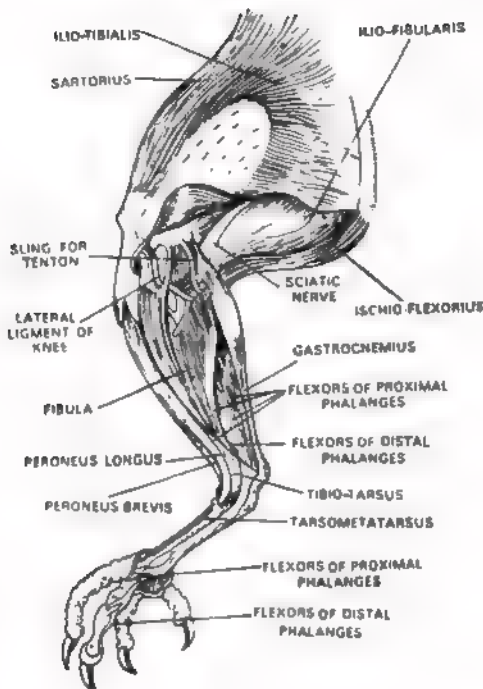


Fig. 7.26. Muscles of hind leg and perching mechanism

muscles that act as lateral rotators. The posterior muscles (**retractors**) of the hip-joint are the main locomotor muscles. These lie behind the hip-joint and include several muscles such as the **posterior ilio-tibial**, **ilio-fibular**, **caud-ilio-flexorius**, **pubischio-femoral**, **ischio-femoral**, and **caud-ischio-femoral**. Some of these also act as lateral rotators with obturator muscles.

The **knee-joint** comprises three sets of ligaments and a pair of lunate cartilages called **menisci** (singular **meniscus**). The three ligaments are known as the **lateral**, **medial** and **cruciate** according to their positions. The **inter-tarsal joint**, that allows movements of flexion and extension, is like the knee-joint and consists of a very strong capsule and lateral and cruciate cartilages. On the lateral side there is a **meniscus**. Following are the muscles of this joint, the **gastrocnemius** along with the flexor muscles of the toes lying behind the tibia (Fig. 7.26); the **tibialis-anterior** on the front of the tibia and acting across the intertarsal joint, and the **extensors** of the toes also lying on the front of the tibia.

Perching Mechanism. Mainly the calf muscles are responsible to bring about flexion of the toes during perching and form an elaborate system of tendons attached to phalanges. These tendons act as a single unit and there is an interlocking arrangement by which the flexion is maintained by the weight of the body during sleep. The perching function has often been assigned to **ambiens**, a slender muscle that arises on the pectineal process of the ileum and is continued over the kneecap into a tripartite **flexor** of the fore toes, but actually the **ambiens** plays only a minor role in perching (mainly flexion of the second toe) and can be cut off without loss of perching ability.

Several leg muscles notably the big "calf" muscle (*gastrocnemius*) and the *peroneus longus* on the anterior aspect of the *crus*, assist in perching, but it is chiefly the action of the *flexor of the digits* that accomplish the tight grip of the foot on the perch. These flexors are eight separate but co-ordinated tendons, six to the fore toes and two to the hallux or hind toe. A nerve centre on the plantar surface of the foot initiates the grip reflex when the foot touches a perch. Several other muscles act as extensors to open the toes. It should be noted that only the tendinous parts of muscles reach the toes, an important measure for heat-conservation.

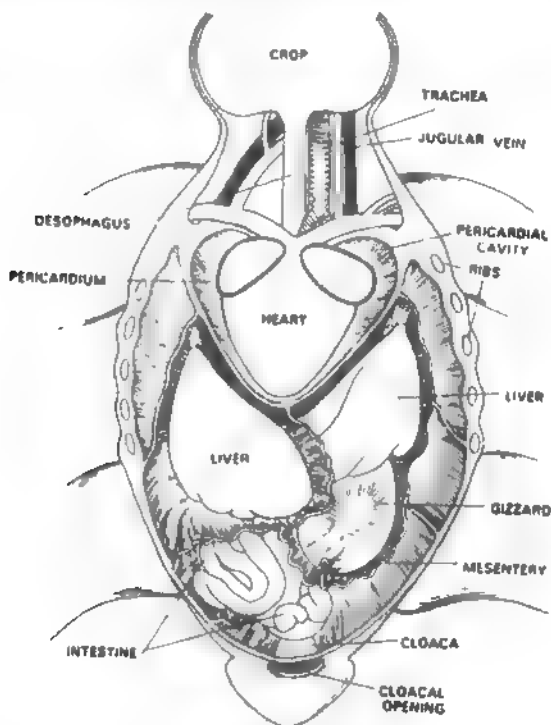


Fig. 7.27. Coelom and viscera of pigeon

COELOM AND VISCERA

Beneath the skin are located thin layers of abdominal muscles corresponding to those of other vertebrates, and internal to this is the *parietal peritoneum* generally impregnated with streaks of fat. The peritoneum lines a cavity, the *coelom*, into which are lodged the various organs of the body cavity, the *viscera*. The small cavity posterior to the sternum is the *peritoneal cavity*. If an attempt is made to expose the body cavity and study the viscera, its different parts will be seen suspended in the body cavity by *mesentery*. There is a mesentery extending from the gizzard to the ventral body wall to the left of the median line. This is the *ventral ligament of the gizzard*, named the *greater omentum* in many text books. But as it is not homologous with the greater omentum of mammals the name is not used here. Anteriorly the ventral

ligament is continuous with the **falciform ligament** of the liver which extends from the median ventral region of the liver to the midventral line of the body wall and inner surface of the sternum. It is this that is first visible the moment an attempt is made to lift the sternum. The falciform ligament and the ventral ligament of the gizzard together constitute a partition which divides the peritoneal cavity into a large right portion and a small left portion. This division does not occur in other vertebrates. In the partition runs a small vein extending from the mesenteries into the liver.

Immediately dorsal to the sternum is situated the delicate pericardial sac containing the heart. The space between the pericardium and the heart is the pericardial cavity, itself a portion of the coelom. The heart has descended posteriorly and a pericardial sac has been formed on the anterior face of the transverse septum. On its ventral face the pericardial sac is in contact with the inner surface of the sternum and anteriorly and laterally it is also in contact with the inner surface of the body wall, hence only the posterior part of the pericardial sac is free. From the point where the pericardial sac meets the lateral body wall a membranous partition extends obliquely posteriorly on each side. This is the **oblique septum**. It contains a large air-sac. It stretches across from the lateral body wall to that part of the pericardial sac which is derived from the transverse septum, and thus divides the pleuroperitoneal cavity into anterior and posterior portions. That part of the original pleuroperitoneal cavity left anterior to the oblique septum consists of two pleural cavities one on each side of the pericardial cavity. The part posterior to the oblique septum is the peritoneal cavity. Thus the coelom of a bird consists of four chambers, the pericardial cavity, the two pleural cavities and the peritoneal cavities.

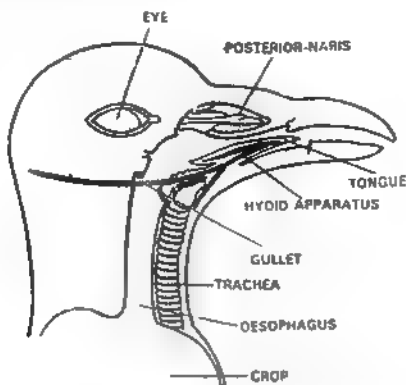


Fig. 7.28. Diagrammatic section of the head of pigeon showing the structure of the oral cavity

Each pleural cavity lodges a reddish flattened organ, the **lung**. The lung of the bird is a spongy mass not hollow. The part of the peritoneum surrounding the lung is the **pleura**. The viscera of the peritoneal cavity includes the **liver**, consisting of right and left lobes. It is a solid organ of dark red colour lying behind and at the sides of the heart. The pericardial sac rests between the two lobes of liver, which are attached to the pericardial sac by the **coronary ligament**. To the left and slightly covered by the left lobe of the liver is the **gizzard**, a large, hard, round structure. Between the gizzard and the liver passes the **gastrohepatic ligament**. The **mesogaster** connects the gizzard with the dorsal body wall. The soft **proventriculus** extends anteriorly from gizzard. The proventriculus and the gizzard together correspond to the stomach of the other vertebrates. They are specialized regions of the stomach correlated with the absence of teeth. From the stomach at the place where the proventriculus and gizzard join the **small intestine** arises. The first portion of this, the **duodenum**, makes a long U-shaped

loop posteriorly. The beginning of the duodenum is attached to the right lobe of the liver by the **hepatoduodenal ligament**. Between the two sides of the duodenal loop stretches the **mesoduodenum**, a portion of the mesentery of the intestine. In this lies **pancreas** between the two limbs of the loop. From a deep depression in the dorsal surface of the right lobe of the liver the two **bile ducts** (there is no gall bladder) emerge and pass into the duodenum. The left bile duct is the shorter and stouter of the two and enters the left limb of the duodenum about half an inch beyond the gizzard. The more slender right bile duct passes to the right limb of the duodenal loop. There are three **pancreatic ducts**, all of which pass from the right side of the pancreas into the right limb. The ducts are easily visible on stretching the mesentery.

The small intestine is much coiled and supported by the mesentery. Near its termination the intestine turns toward the median line, widens slightly and runs toward the posterior end. At about the middle of the peritoneal cavity it passes without enlargement into the **large intestine**. The point of junction of the large and small intestine is marked by a pair of small lateral diverticula, the **caeca**. The large intestine is short and soon passes into the **cloaca**. Owing to the absence of pubic and ischial symphysis in birds, the cloaca does not pass through the ring of the pelvic girdle, but may be traced directly to the **anus**. There is no urinary bladder. In the female specimen the single left oviduct may be seen entering the oviduct. The single ovary (left) is situated in the anterior part of the peritoneal cavity dorsal to the gizzard. On turning the gizzard far forward a dark, round red body, the spleen, may be found.

DIGESTIVE ORGANS

Oral Cavity The roof and the floor of the oral cavity are bounded laterally by horny beaks of epidermal origin which encase the jaws, which are without teeth. The roof of the mouth cavity bears a pair of elongated **palatal folds** with free fimbriated margins. This corresponds to the hard palate of mammals, but has a deep **palatal fissure** in the median line. The palate, therefore, is a split palate. Dorsal to the palatal folds occur the **posterior nares**, a pair of long narrow apertures, lying side by side in the roof of the mouth. The anterior two-third of their length is hidden by the palatal folds of the mucous membrane. The floor of the mouth cavity is occupied by the pointed **tongue** which is narrow and triangular with a sharply pointed tip. Posteriorly it is produced into two lobes fringed with fine horny processes. The tongue is not very muscular. Numerous glands open into the oral cavity in birds but are very small.

In the roof of the pharyngeal cavity just posterior to the caudal ends of the palatal folds there is a median aperture, the opening of the paired **auditory tubes** (Eustachian tubes). Each tube extends from this opening to the cavity of the middle ear. The tube and cavity are derived partly from an evagination from the first **visceral pouch**. In birds, unlike other vertebrates the two auditory tubes unite at the point of communication with the pharynx; i.e., there is a single aperture of the Eustachian tubes. Posterior to this opening the roof bears a pair of folds with fimbriated borders constituting the **soft palate**. They hang down like a curtain into the pharyngeal cavity. Immediately posterior to the caudal end of the tongue there is a hardened elevation, the **laryngeal prominence**. In the centre of this lies an elongated opening, the **glottis**. The margin of the glottis is also fimbriated, and immediately posterior to it on each side is a fringed fold. The walls of the glottis are supported by **laryngeal cartilages**. Behind the glottis there is a large wide opening, the **gullet**.

The gullet opens into a long tube, the **oesophagus**, that runs back through the neck to the stomach. In the neck region it enlarges to form a thin-walled bilobed sac, the **crop**. It again becomes thick-walled as it enters the thorax (Fig. 7.30). Birds swallow their food whole and collect it in the crop which has great power of distension. The food is passed on to the stomach in small quantities. All birds do not have crop. The **proventriculus** is the continuation of the oesophagus lying dorsally to the left liver lobe. It is comparatively wide and has thick glandular inner lining that produces the **gastric juice**. To its right side is attached the spleen. The proventriculus opens into the **gizzard** which is a large hard body flattened laterally, forming a biconvex structure. Its walls are thick and muscular and its inner lining is horny. The cavity is very small and

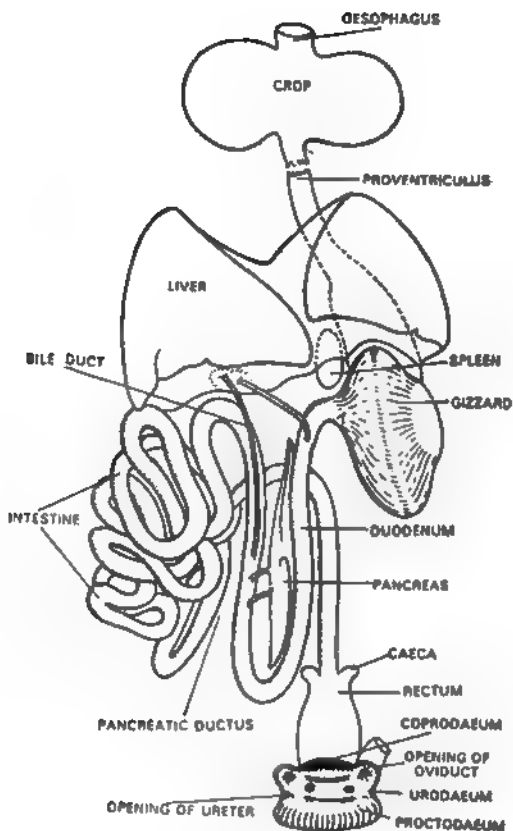


Fig. 7.39. The digestive organs of pigeon.

often contains small pieces of stones. These pieces help in crushing the food as the strong muscles of the gizzard work. The gizzard thus becomes a powerful **grinding mill**. The oesophagus opens into the gizzard dorsally, slightly to the left side, while the duodenum leaves it a little to the right side of the same spot. The proventriculus and gizzard together correspond to the stomach of other vertebrates. They are specialized regions of the stomach correlated with the absence of the teeth. From the stomach, at the place where proventriculus and gizzard join, the small intestine arises. The first portion of this is the **duodenum**, a U-shaped loop. Between the two limbs lies the **pancreas**. The beginning of the duodenum is attached to the liver by the hepatoduodenal ligament. Between the two limbs stretches the **mesoduodenum**, a part of mesentery lodging the pancreas.

The duodenum passes into the **small intestine** which is a convoluted tube of uniform diameter. It is the longest part of the alimentary canal and leads into the rectum. The small intestine is similar to that of the lower tetrapoda in its construction, but is more highly convoluted; on the average the length of its coils is eight times more than that of the whole body. This great elongation, it is presumed, is correlated with the great

activity and high metabolic rate of birds which results in an increased demand of food and consequent requirement of additional absorptive surface in the intestine

The **rectum** is the terminal portion of the intestine. At its junction with the intestine are situated two caecal processes, the **rectal diverticula**. The rectum opens in the cloaca posteriorly, with which it is not marked off separately. The birds have no functional urinary bladder, as such urine and faeces are mixed to be discharged as a slushy material usually called **guano**.

The liver and **pancreas** are two glands associated with the digestive system. The liver is two lobed in pigeon. Of these the right lobe is the larger. There is no gall-bladder in birds. The two bile ducts emerge directly from a deep depression in the dorsal surface of the right lobe of the liver. The left bile duct is shorter and stouter of the two and enters the left limbs of the duodenum about half an inch beyond the gizzard. The right bile duct is slender and passes to the right limbs of the duodenal loop.

The pancreas is a compact pinkish gland lying in the loop of the duodenum. It gives rise to three pancreatic ducts, all of which pass from the right side of the pancreas into the right limb of the duodenal loop. One of these arises from the anterior part of the pancreas and passes obliquely forward, entering the duodenum near the anterior termination of the right limb of the loop. The other two ducts emerge from the middle of the pancreas and pass across the right limb of the duodenum. These ducts are easily visible if the mesentery is spread.

RESPIRATORY SYSTEM

The respiratory system in birds is fairly complicated. The slit-like **external nares** open into the base of the bill, surrounded by a swollen sensitive **operculum** (in pigeon) or by a soft membrane the **cere** (hawks). The external nares open into the olfactory chamber opening directly into the pharynx by **internal nares**. The glottis is the opening that leads into the **air-tube** or **trachea**. It opens into the **larynx**, which is the expanded chamber at the top of the trachea. The walls of the larynx are supported by cartilaginous pieces. On each side of the larynx there is a practically ossified **arytenoid cartilage** and on the ventral side lies the larger triangular **cricoid cartilage**, which extends dorsally terminating by much narrowed ends. Between the two dorsal ends of the cricoid cartilages there is another **median cartilage**, the **procricoid**, which is in contact with the posterior ends of the arytenoids. The arytenoids are derived from certain of the brachial arches while the cricoid and procricoid cartilages are modified anterior-most tracheal cartilages. Morphologically the structure of the larynx of the birds is similar to that of other vertebrates, but in birds the larynx does not produce sound, which is produced by another structure called **syrinx**, situated below in the **trachea**.

The **trachea** or **windpipe** is a tube which commences in front at glottis, runs back along the neck, and divides, in the thorax, into two **bronchi**, entering the right and left lungs respectively. It is surrounded by a series of closely set **tracheal rings** which are ossified ventrally and cartilaginous dorsally. In the anterior part of the neck the trachea is ventral to the oesophagus, further back it lies along its left side. In the thorax, where it again lies ventral to the oesophagus, it divides into two bronchi, which run outwards and backwards to enter the lungs on the ventral surface and near their anterior ends.

The **syrinx**, or '**lower larynx**', is the organ of voice of the pigeon, and is formed by the dilated hinder end of the trachea, before the commencement of the bronchi. The walls of the syrinx are supported by the last tracheal ring and the first brachial half-ring. The cavity of the syrinx is named the **tympanum**. In the dorsal walls of the tympanum a slight vertical fold is present in the median dorsal line, extending forward from the level of the bifurcation of the trachea. This fold is called the **semilunar membrane** (**membrana semilunaris**) and its vibrations are said to produce the voice. The mucous membrane lining the inner wall of the commencement of each bronchus is called the **membrana tympaniformis internalis** (Fig. 7.31). Running across the tympanum there is a slender bar of cartilage, the **pessulus**, in the substance of the **membrana semiluna-**

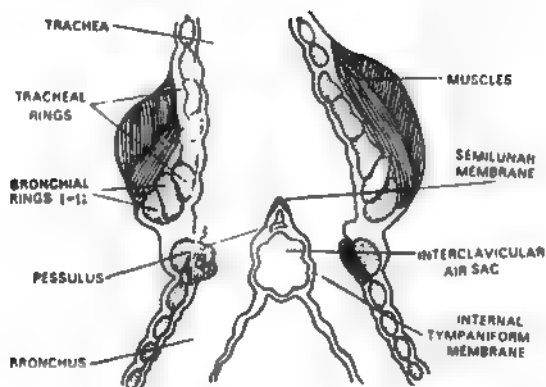


Fig. 7.31. Longitudinal section through the syrinx of a bird.

bronchi. The result is that a series of anastomosing tubules forming circuits within the lungs are formed. The inner surface of the parabronchi often work as respiration surfaces. This is quite unlike the mammalian lung in which blind pouches (alveoli) provide the respiratory surfaces. Thus a relatively small and inelastic lung in birds is able to meet the extraordinary demand of oxygen, which is greatest among all the vertebrates.

Air-sacs. The lungs of all modern birds are characterised by the presence of remarkable system of supplementary air-sacs (*cellulae aereae*) which facilitate the circulation of air through the lungs, but in themselves are not directly respiratory in function, as is evident from the paucity of capillaries over their surfaces. The air-sacs are large thin-walled sacs occupying spaces between the viscera, beneath the skin (in pelicans), between the muscles supporting the connective tissue between and around the joints of the cervical vertebrae and penetrating even into the pneumatic cavities of the hollow bones.

There are nine air-sacs in the pigeon, a median interclavicular, a pair of cervical (or Prebronchial), two pairs of thoracic intermediate, and a pair of abdominal or posterior. The abdominal air sacs are a pair of large sacs, with very thin transparent membranous walls which lie along the dorsal wall of the pelvic cavity, ventral to the

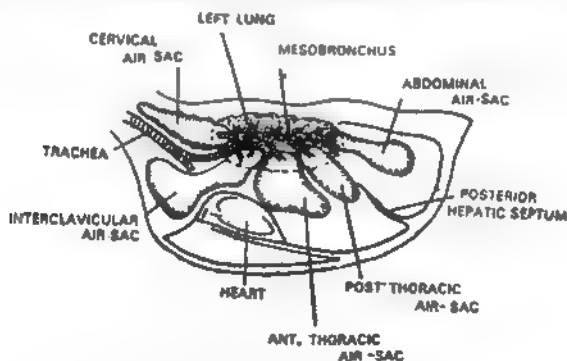


Fig. 7.32. Air-sacs and left lung of a bird, lateral view.

kidneys but dorsal to the intestine. At the hinder end of the abdomen they come close up to the ventral surface when inflated. Each communicates with the posterior border of the corresponding lung, near its outer angle (Fig. 7.33). The **posterior thoracic air-sacs** are a pair of rather smaller sacs lying along the outer sides of the anterior ends of the abdominal sacs. They lie mainly posterior to the lungs, but overlap the ventral surfaces of their hinder ends. Each communicates with the outer and posterior angle of the corresponding lung (Fig. 7.32). The **anterior thoracic air-sacs** cover the ventral surfaces of the anterior two-thirds of the lungs, and extend back so as to overlap the posterior thoracic sacs. They lie at the sides of the thorax, and are in extensive contact with the ribs and with the pericardium. Each communicates with the ventral surface of the lung, rather in front of the middle of its length, and not far from median plane of the body (Fig. 7.32). The **interclavicular air-sac** is a medium sac formed by the fusion of two originally distinct ones. It consists of (i) a median portion, which surrounds the hinder end of the trachea, and can easily be seen in the angle between the two clavicles; and (ii) lateral diverticula, one of which runs forward along each side of the trachea, while other passes outwards beneath the coracoid, and open into large **axillary air-sacs** in the neighbourhood of the shoulder joints, which communicate with the cavities of the humerus bones. The interclavicular air-sac opens into the ventral surface of each lung, immediately in front of the point of entrance of the main bronchus. The cervical air sacs (Figs. 7.30, 7.32) are much smaller and lie in front of the lungs at the base of the neck, alongside the vertebral column. They communicate with the anterior angles or apices of the lungs.

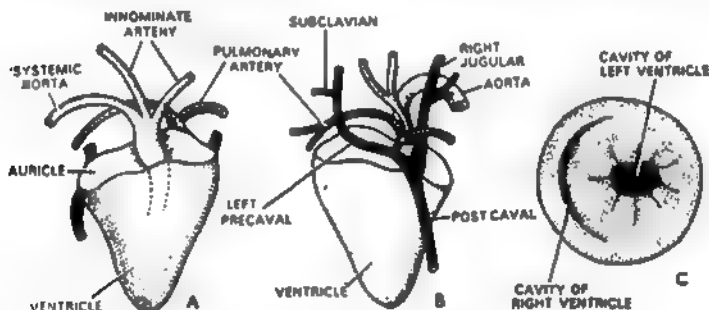


Fig. 7.33. Heart of pigeon. A, dorsal view; B, ventral view, and C, cross-section of ventricle.

The lining of the air-sacs is generally smooth and cannot act as respiratory space, although the sacs may aid as cooling devices in the regulation of the body temperature. Nevertheless they play important role in respiration. The air-sacs draw air in and force it out, of course, aided by other means (see below), and gaseous exchange takes place when the air goes to the air-sacs through the lung as well as on its return.

Ventilation of Lung. When the pigeon is at rest air is drawn in (inspiration) by a forward and upward movement of the ribs and sternum which expands the trunk capacity. The breathing mechanism in the birds is that of a suction pump. This movement alternates with the depression of the sternum and the air is pumped out (expiration). The actions are produced partly by the abdominal and partly by intercostal muscles. During flight when the weight is supported by the wings and the sternum is rendered immovable, the same effect seems to be produced by the elevation and depression of the back. The avian lung empties completely with each breath, no residual air being left in. In the pigeon in flight air-sacs are also emptied completely with each breath, but not when the bird is at rest. The birds that sing a long uninterrupted song (winter wren) are believed to utilize reserve air in air-sacs. When submerged water birds also do the same.

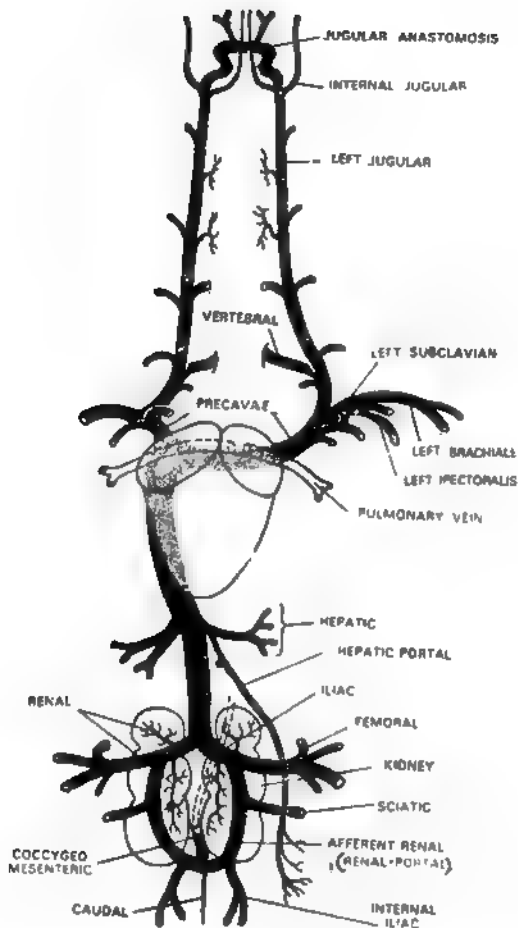


Fig. 7.35. Venous system of pigeon.

the left auriculo-ventricular aperture (Fig. 7.34) a circular opening guarded by the left auriculo-ventricular valve (the mitral valve) consisting of three muscular flaps projecting into the ventricle. The major portion of the heart is formed of the right and left ventricles, which together constitute a muscular thick-walled cone having a pointed apex directed posteriorly and a broad base directed anteriorly, internally the two ventricles are completely separated from each other, but the division between them is indistinct externally. The interventricular septum passes obliquely in such a way that the left ventricle becomes larger of the two and includes the whole of the apex of the heart. The right ventricle is thin walled and wraps around the left ventricle. In a transverse section it appears crescentic lodging the left ventricle in its concavity. The left ventricle has thick spongy walls enclosing a somewhat circular cavity. Into the

extreme anterior end of the left side of the ventricle lies the **aperture of the pulmonary artery**, guarded by three **semilunar valves**. Into the left auricle is situated the **aperture of the aorta** at its anterior end. This aperture is also guarded by three semilunar valves (Fig. 7.34).

Veins. The veins include two **precaval** and one **postcaval**, all opening into the right auricle. The right anterior vena cava (Fig. 7.35) is a small thin-walled vessel that collects blood from the right side of the head, the neck, the right wing and the right side of breast through the right **jugular vein** and the right **subclavian**. The right **jugular vein** (Fig. 7.35) that runs along right side of the neck, close to the vertebral column and almost behind the oesophagus. Near the angle of the jaw it divides into the **external** and **internal jugulars**. The **external jugulars** unite with each other on the under surface of the base of the skull forming a loop, the **jugular anastomosis**. The **internal jugular** of each side collects blood from the brain etc. During its course the right jugular receives blood from the sides of the neck, the crop and the vertebral column of the region by the **oesophageal** and the **vertebral** and **cervico-cutaneous** veins. The right **subclavian vein** is formed by the confluence of the two following veins: the **right brachial vein** returning blood from the right wing and the **right pectoral vein** returning blood from the large pectoral muscles. It also receives a delicate **internal mammary vein**, that runs along the inner surface of the thoracic wall, before entering the precaval. The left anterior vena cava is corresponding to that of the right side. The posterior vena cava (Fig. 7.35) is formed by the union of the two **afferent renal veins** a little behind the liver. In the region of the liver it receives the **hepatic veins**.

Posterior Veins. A small narrow blood vessel the **caudal vein** collects blood from the tail region. It bifurcates to form two **afferent renal veins** (renal portal of amphibians and reptiles) that run over the kidneys sending branches into them. The **afferent renal** (renal portal) veins (Fig. 7.35) are formed by the bifurcation of the **caudal vein**, like the renal portals in others but they are not portal functionally, they do not break up into double set of capillaries as in the reptiles and lower vertebrates. Each passes onwards over the kidney, sending off a few branches to the kidneys (carrying blood to that organ), and receiving a prominent **femoral vein** returning blood from the leg, between the first and second lobes of the kidney. A delicate **scialic vein** has been observed in some cases between second and third lobes of the kidney, but it is not a regular feature. The **efferent renal (iliac) vein** (Fig. 7.35) formed by the union of the **femoral** and the **afferent renal** leaves the kidney at its inner border, between its anterior and middle lobes and then runs forwards, joins its fellow of the other side and forms the **posterior vena cava**. The **internal iliac veins** are a pair of small vessels, each of which joins the **afferent renal** coming from the inner surface of the pelvic region. The **coccygeo-mesenteric vein** arises from the caudal veins before it bifurcates into the **afferent renals**. It runs parallel to the rectum and intestine, to a little distance and opens into the hepatic portal. The **posterior mesenteric** (Fig. 7.35) vein returns blood from the hinder part of the body cavity and mesentery, etc. into the **coccygo-mesenteric** just near its root.

Hepatic Portal System. This system presents the same structure as found in other vertebrates. The hepatic portal vein is formed by a number of narrow blood vessels coming from the various organs of the digestive system. On reaching the liver it bifurcates into two branches, one going to each lobe. The blood from the greater part of the alimentary canal is conveyed to the liver whence it goes to the heart. From the margin and left side of the gizzard and proventriculus arise the **left and median gastric veins** opening into the hepatic aorta. From the small intestine it receives the **superior mesenteric**, from the duodenal loop, pancreas and right side of the gizzard it receives the **gastroduodenal**, and from the large intestine, etc it receives the **inferior mesenteric**. The **pulmonary veins** are the only two very short blood vessels that bring blood back from the lungs and open into the posterior surface of the left auricle. Each emerges from the lung and passes toward the heart immediately posterior to the pre-caval veins. Sometimes two pulmonary veins may arise from each lung, the veins pass to the dorsal side of the bases of the precavals and enter the left auricle.

Arteries. In the birds all the great arteries spring directly from the ventricle and are situated between the two auricles. There are two arterial trunks, the larger medially

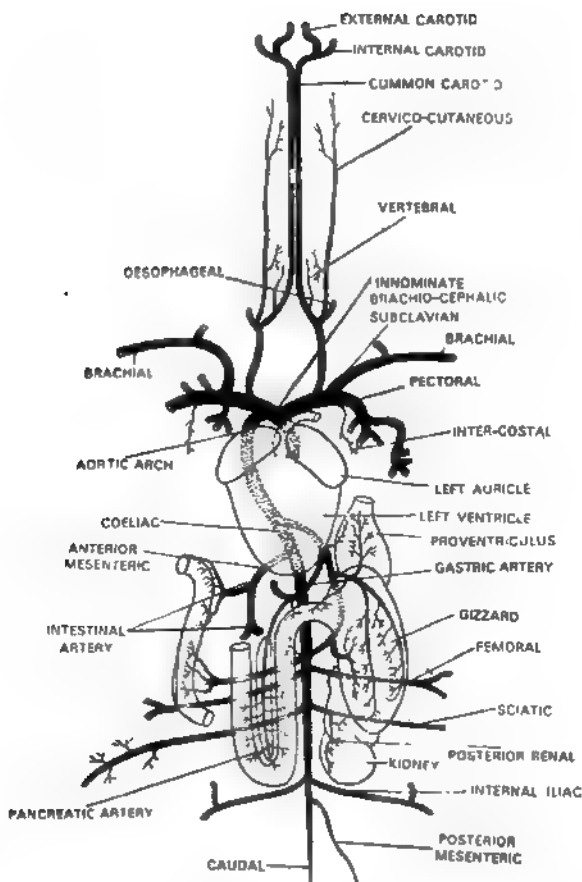


Fig. 7.37. Arterial system of pigeon.

round the antero-lateral region of the sternum, enters the great pectoral muscle, which it supplies. The right innominate gives out exactly similar branches.

The **aorta** (Fig. 7.37) arches over to the right side and runs backwards crossing the right pulmonary. Then it runs backwards in the mid-dorsal line forming the **dorsal aorta**, giving off a number of branches. The **coeliac artery**, a median vessel, arises just as the aorta emerges below the ventricle. It supplies the stomach gizzard and part of the intestine. The **anterior mesenteric** arises about a quarter of an inch posterior to the coeliac artery, runs back into the mesentery and supplies the intestine. The **anterior renal arteries** are a pair of small vessels arising from the aorta, a little anterior to the first lobe of the kidneys. Before entering the substance of the anterior lobe of the kidney each gives off a branch going to the testes in the male, and in the female only the one on the left side gives off a branch supplying the ovary. The **femoral arteries** are a pair of prominent blood vessels arising opposite the anterior lobes of the kidneys.

in birds haemorrhage of blood vessels is not infrequent. The rate of heart beat differs greatly in different species and under different conditions. Odum has carried out experiments on heart beat of certain birds. According to him in black-capped chickadees during sleep (completely relaxed) the rate varied from slightly less than 400 to over 600 beats per minute. Under stress this rate was doubled. In canary under excitement it may exceed 1,000 per minute. It is about 300 beats per minute in the fowl.

The body temperature of birds is also variable. In primitive birds like New Zealand Kiwis the temperature is lower at about 100°F but it may reach a maximum of 112°F in most passerine birds. In most birds the temperature varies with the time of the day being highest about mid-day and lowest during the night in diurnal birds. The temperature varies with activity, arising with exercise. The emptiness of stomach may also cause fluctuation of temperature. But in all cases the fluctuating range may be as much as 8 to 10 degrees say from 102°F to 112°F in passerines. In house wrens the temperature can fluctuate from less than 90° to 115°F., but range of about 102° to 112°F is more normal.

Temperature Regulation. Birds live in varying environmental conditions, to which they adjust by many ways. The birds that live in Arctic Zone conserve heat by being densely feathered. The feather coat insulates the body. Sleeping birds commonly tuck their bills in their feathers in cold weather to reduce loss of heat in breathing, and the breathing rate and general metabolism are lowered. Shivering is another method that is employed to adapt to sudden cold, because it converts muscular energy into heat. The problem of preventing heat loss through unfeathered portions of the body in cold weather has not been worked out fully. It has, however, been suggested that such areas have restricted circulation and low thermal conductivity.

In warm weather the air-sacs of the birds are used as a chief means of dissipating excess heat. The birds have no sweat glands in the skin. The heat and water passes on to air-sacs from which excess of heat is removed through the lungs and mouth. In hot weather a bird is usually seen gaping with open mouth. It is not panting for breath, but is speeding up dissipation of internal heat by an increased breathing rate and faster evaporation of moisture.

In some species young birds cannot regulate body temperature at hatching, and at first, need more or less complete brooding. They are, therefore, poikilothermous at birth, but as soon as the feathers develop the homoithermous condition progresses rapidly. In house wren, for instance, this condition is established well at about the age of nine days.

NERVOUS SYSTEM

The nervous system of birds is constructed on the reptilian plan, but there are some notable differences. In the brain of the bird the olfactory bulbs are much smaller in comparison with the hemispheres. This change definitely puts birds on a higher evolutionary level than reptile in which the olfactory bulbs form a prominent part of the brain in relation to the cerebral hemispheres. This advancement, however, is followed by a serious backward step. The bird's hemispheres are large but the cortex is reduced in amount and is more primitive in its structure. As is clearly understood the cortex is the seat of the highest mental activity, its reduction in size and elaboration suggests a falling-off of powers of learning and of making adjustments to new conditions. The increase in the size of the hemispheres indicates an enlargement of instinctive life, and everybody knows that birds with their nest-making, their migrations and homing habits live a very complex life of instinct. In this case the domination of inherited habits is not complete. Birds can modify their habits in many ways.

Brain. On anatomical considerations the olfactory lobes are small in correlation with the poorly developed sense of smell. The optic lobes are smooth ovoid large bodies in keeping with the well developed visual sense of birds. Their sight is keen and stereoscopic. The **cerebrum** is large but is relatively smooth and lacks the deep fissures characteristic of the mammalian brain. The large cerebral hemispheres separated by a deep **sagittal fissure** overhang posteriorly concealing the diencephalon completely, with the exception of the delicate **pineal body** seen on the posterior end of the sagittal

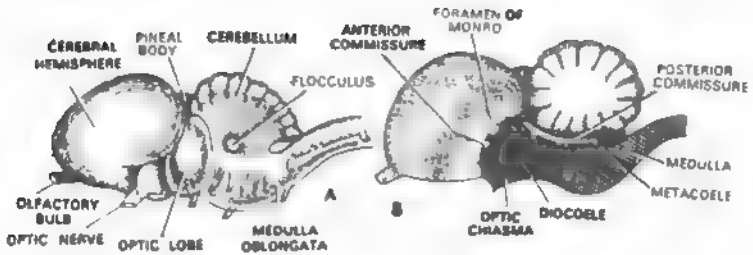


Fig. 7.39. A lateral view (A) and sagittal section of brain (B) of pigeon

fissure. The **cerebellum**, which is responsible for precise control movements, is well developed. It has a large median portion and two small lateral lobes, the **flocculi**. The whole brain is packed into a comparatively small space in the cranium, compressed posteriorly by the extremely large orbits. The brain is short and broad and is strongly curved in correlation with the bipedal gait. The **primary flexure** occurs in the region of the mid brain, with the result that the posterior part of the brain is bent nearly at right angles to the anterior. The **nuchal flexure** and the **pontal flexures** are also visible. The nuchal bends the medulla at an angle to the spinal cord and the pontal flexure in the region ventral to the cerebellum bends the brain in the opposite direction from the other two flexures. The posterior region of the brain is the **medulla oblongata** that continues into the spinal cord. The **optic chiasma** is, as usual, a crossing formed by optic nerves on the ventral side of diencephalon. Behind the chiasma lies a median process, the **infundibulum**.

The cavities or ventricles of the brain are reduced very much. The **diacoele** or the third ventricle is the cavity of the diencephalon (not seen externally due to the overgrowth of cerebral hemispheres and the cerebellum). It is a narrow vertical cavity bounded laterally by the **optic thalami** and opening in front by the **foramen of Monro** into the **paracoeles** or the ventricles of the hemispheres. The cavities of the optic lobes are called **optocoeles** opening in the centre into a narrow passage the **iter**, the cavity of the mid-brain. The cavity of the medulla oblongata is the **metacoele**, and is relatively larger and rooted over by the posterior **choroid plexus**.

There are twelve pairs of **cranial nerves** in the pigeon. These include the olfactory, optic, trochlear, oculomotor, abducens, trigeminal, facial, auditory, glosso pharyngeal, vagus, the spinal accessory and hypoglossal. The course of these nerves is similar to those of other vertebrates. The spinal accessory passes out with the vagus and is distributed to certain muscles. The hypoglossal is found just posterior to the vagus and is distributed to certain neck muscles. It also sends a branch to the tongue.

The **spinal cord** is reduced in length in birds due to the reduction of the vertebral column. It presents two enlargements as in reptiles and tapers posteriorly. The **cervical spinal nerves** arise at segmental intervals and lie between the skin and vertebral column. Their number corresponds with the number of vertebrae in the neck region. The ventral branch of the last cervical nerve together with that of the first of the trunk form the **brachial plexus** to the wing. This is a network formed by the union of branches of four stout nerves, which receives a small branch from the succeeding nerve. The next five pass out between the ribs. After these there is a **lumbosacral plexus**, divisible into three parts, the **lumbar**, the **sacral** and the **puddendal plexus**. The lumbar plexus is formed by three nerves, sending nerves into the thigh. The sacral plexus is formed by five nerves, the first of which is the third of the lumbar plexus. These five form a large **sciatic nerve**, which passes along the dorsal side of the thigh between muscles and proceeds down the legs alongside the femoral artery and vein. The remaining spinal nerves posterior to the sacral plexus form the **puddendal plexus** from which nerves pass obliquely to the tail and cloacal region (Fig. 7.41).

The **sympathetic system** consists of a chain of two cords and segmental ganglia on each side. One of the cords lies ventral to the head of the rib, the other dorsal to it. A

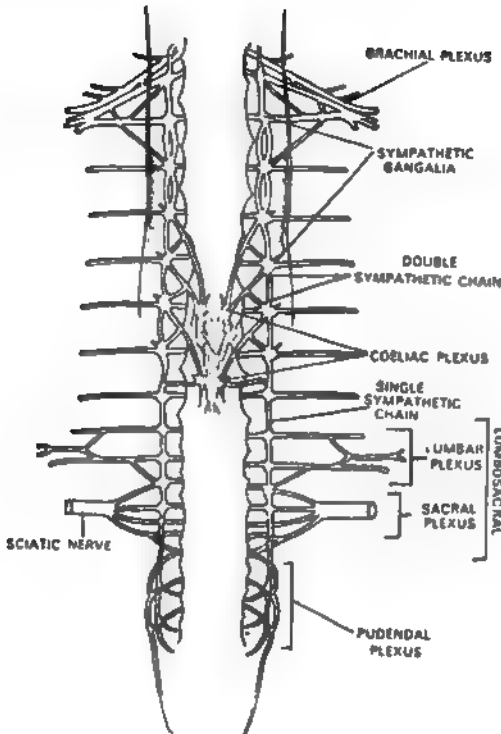


Fig. 7.4f. The spinal nerves and sympathetic system of pigeon

sensitive muzzle The nasal passage is not lined by sensory epithelium as in mammals. There are two **nasal cavities** in the pigeon separated by a median septum, from which three swellings, the **turbinals** or **conchae** project into the nasal cavity. The three turbinals are in a row. Of these the first two are large ones and the third and most posterior one consists of a small round swelling on the roof of the cavity in close contact with the posterior end of the second concha. Only the third concha is provided with olfactory epithelium. Beyond the conchae the nasal passages open into the pharyngeal cavity. The degeneration of the olfactory sense is probably correlated with the increased specialization of other senses, such as vision.

The taste discrimination which is associated intimately with smell is also uncertain in birds. There is a definite scarcity of taste buds; a few scattered over the palate or on the usually undifferentiated tongue permit some taste discrimination, but a majority of birds bolt food material quickly without tasting or moistening them before swallowing. In young birds the food is often placed far back in the throat, so that taste buds, salivary glands and even much differentiated tongue may be superfluous. Exceptions occur among sticky tongued birds like flickers and humming birds which have salivary glands to provide the adhesive for gathering up small insects, and among swifts, which use a glue like salivary secretion for nest building. The pigeon being a seed-eater does not have well-developed sense of taste although some others (insect-eating and cat on-feeding birds) may have fairly discriminating sense of taste.

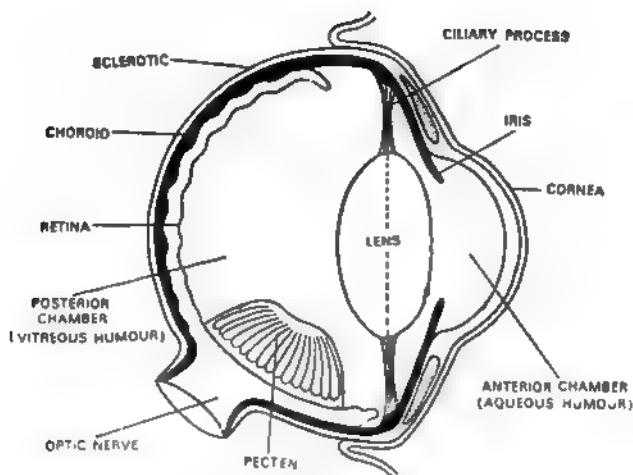


Fig. 7.42. Sagittal section of eye of a bird

Vision. The existence of birds depends upon a keen sense of sight. Having mastered the air the need for sharp and discriminating vision is readily apparent. The structure of the eye is like that of any other vertebrate with a couple of distinctive features. There are two eyelids of which the upper one is only slightly movable but the lower one is very freely so. A nictitating membrane (or third eyelid) is also present. It is a fold at the anterior angle of the eye, lying within the other eyelids, between them and the eyeball. It can be pulled obliquely downward and backward over the front of the eye with great rapidity. This semitransparent third eyelid mainly functions for cleaning the eyeball and also acts as a protective device. When birds are facing or flying against the wind the nictitating membrane is particularly protective. In nocturnal birds it cuts down the glare of the sunlight during the day and in aquatic birds it shields the eyes under water.

The eyeball is globular in some and nearly tubular in owls but has the form of a biconvex lens in the pigeon. The cornea and lens both are bulging towards the outer side. A ring of bony sclerotic plates holds the eye in its proper place, and imparts a forward bulge to the cornea. Special muscles alter the curvature of the cornea and

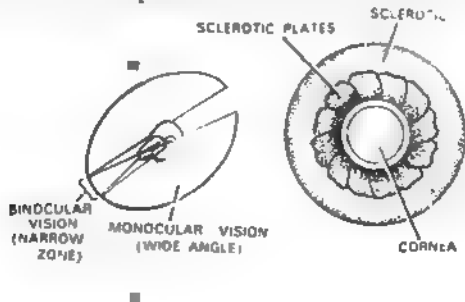


Fig. 7.43. A, front view of the eye of pigeon showing the sclerotic plates, B, diagram showing the range of vision, monocular (M) and binocular (B) in the pigeon.

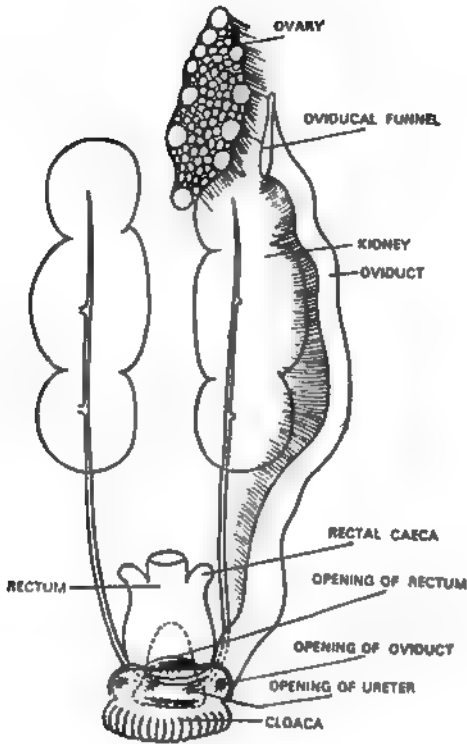


Fig. 7.44. Female urogenital system of the pigeon.

female. To the anterior part of the kidneys are attached elongated yellowish bodies, called the **adrenal bodies**.

Female. In the adult female there is a single ovary and oviduct on the left side. The right ovary and duct are present in the embryo but almost entirely disappear before hatching. The ovary is a mass containing eggs of various sizes, situated at the anterior end of the left kidney. It is suspended in the body cavity by mesovarium. The left oviduct is wide convoluted tube running posteriorly to the cloaca and is attached to the body wall by mesotubarium. The **ostium** is situated in the mesotubarium near the ovary. It is a wide opening with wing-like borders fastened to the mesotubarium. A small remnant of the right oviduct is attached to the right side of the cloaca. The wall of oviduct is glandular. The glands in the middle portion add enveloping layer of albumen and the glands (**shell glands**) in the lower expanded uterine portion add shell to the egg. Pigment is also added here and many birds, for this reason, have pigmented eggs.

The cloaca is an expanded chamber receiving the rectum on its median ventral surface, the left oviduct to the left, the vestigial right oviduct to the right and the ureters dorsal to the oviducts. The cloaca is subdivided into portions. There is a large ventral portion into which opens the rectum. This is called **coprodaeum**, from which a fold separates a dorsal chamber called **urodaeum**, into which open the ureters and oviducts. The openings of ureters are more medial and smaller. Knowing this, it is easy

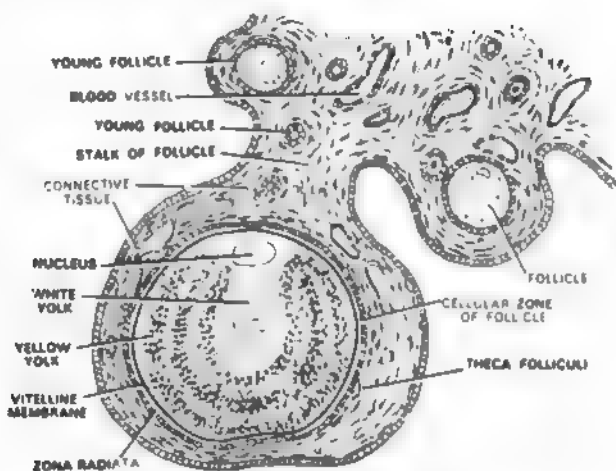


Fig. 7.45. Diagrammatic section through the ovary of pigeon.

to locate the larger opening of the left oviduct. The most dorsal compartment of the cloaca is called **proctodaeum**, a smaller chamber with a raised rim, which opens at the anus. In the anterior wall of the proctodaeum lies the opening of a small pouch, the **bursa of Fabricius**, which seems to be functional in young birds but degenerates with maturity.

Male. The testes are a pair of oval bodies lying in contact with the ventral surface of the anterior lobes of the kidneys. The size of the testes varies considerably with season. The male ducts, **vasa deferentia** (**Wolffian ducts**), spring from the medial border near the posterior end of the testes and pass posteriorly parallel to the ureters. They are slender, convoluted opaque tubes. In the breeding season their hinder ends become swollen to form the **sacculi** vesicles for temporary storage of sperms just before they open into the cloaca. The cloaca in the male is a tubular portion smaller than in the female and the lips of the anus are more protruding. The rectum enters medially and ventrally, the urogenital ducts laterally. The urodæum receives two vasa deferentia instead of the oviduct. Ureters and vasa deferentia open on small papillae in the lateral walls of the urodæum. There is no penis in most birds. Transfer of the sperms to the female during breeding takes place by direct cloacal contact during **copulation**, when the male mounts the back of the female momentarily so that their cloacae are closely appressed and the transfer effected quickly. Copulation is frequent during the **early part** of the breeding season, just prior to and during the egg-laying period, but usually wanes or ceases altogether during the later phases of the nesting cycles.

EMBRYOLOGY OF CHICK

One of the most remarkable features of the development of living organisms is their capacity to undergo great changes in structure without ceasing at any stage. From the single-celled stage right up to the adult vital processes like respiration, nutrition and excretion must continue and development, being dependent on these processes, can progress only so long as it follows paths which maintain them. In the large enclosed egg of birds and reptiles the actual living matter is, at the start, less than one thousandth part of the whole, all the remainder being developed to protection and storage of food and water. Surrounded in this way by most of its immediate requirements, the embryo is spared many of the difficulties of free living forms and can direct

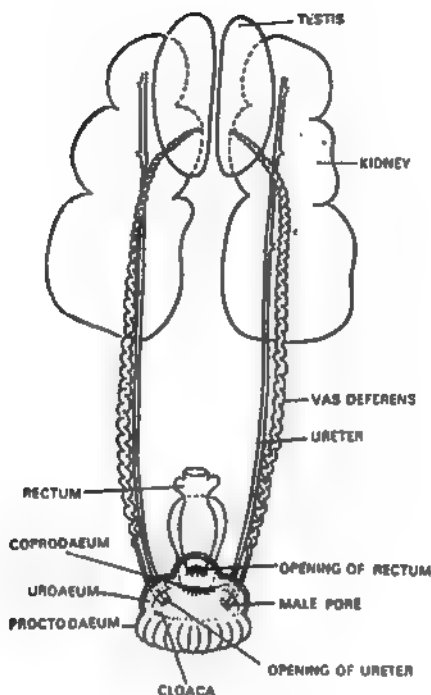


Fig. 7.46. Male urogenital system of the pigeon

its resources towards developing the particularly elaborate form of organization.

Egg. The eggs when released are simple surrounded by a delicate vitelline membrane. Such eggs are passed into the oviduct where they are fertilized if fertilization is to take place (hens regularly and wild birds occasionally lay unfertilized eggs). As the egg passes down it receives a thick envelope of albumen from glands in the middle portion of the oviduct, and then the shell is added from gland (shell glands) in the lower expanded "uterine" portion of the oviduct. In many birds that lay coloured eggs pigment is added by a part of the shell gland. The completed egg (yolk, albumen, shell and pigments) is then ready for deposition.

At the time of laying the hen's egg has the structure described below. The yolk and small quantity of living protoplasm are contained within the vitelline membrane. Immediately inside the shell are two membranes separated at the broad end of the egg to enclose an air-sac. Between these shell membranes and the vitelline membrane lies the albumen or white of the egg. The albumen is of two kinds, a thick gelatinous semi-solid and a thin liquid. The thick albumen forms a closed sac completely surrounding the yolk, and attached at the end of the egg to the shell-membranes. The thin albumen forms a layer between the thick albumen and the vitelline membrane, and another layer between the thick albumen and the shell membrane. Extending from the vitelline membrane to the thick albumen at each end of the egg is a twisted fibrous structure called *chalaza*. Lying between the vitelline membrane and top of the yolk is found a small disc of protoplasm called *blastodisc* or *germinal vesicle*. It is this disc alone (not the entire egg) that undergoes divisions or cleavages. Such an egg is called

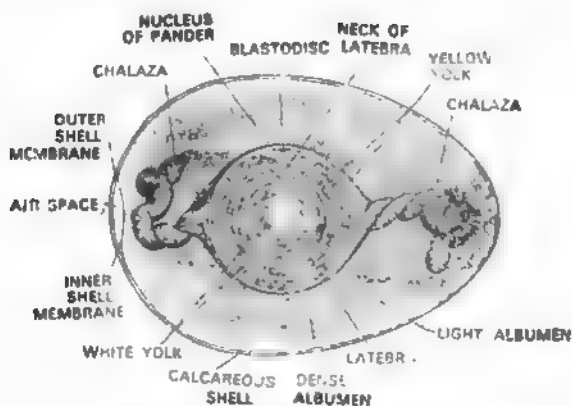


Fig. 7.47. The egg of chick with its membranes.

meroblastic (or discoidal). The blastodisc is constantly kept uppermost by its lesser weight when the egg is turned, producing the characteristic twisting in the rope-like chalaza. Soon after the extrusion of the egg from the ovary the egg and the sperm nuclei unite (fertilization) and the segmentation or cleavage begins within the warm reproductive tract before the egg is laid, but is then arrested until incubation begins, which may be several days to a week or more after oviposition. By the time the egg is laid, however, several divisions of the blastodisc have taken place and it becomes a small disc of cells between the vitelline membrane and the top of the yolk. This disc of cells is termed **blastoderm**.

The structure of the ovum proper is complicated. It is the spherical yellow portion ordinarily referred to as the "yolk" that is the ovum proper. It consists of large amount of yolk with a small protoplasmic patch, the **blastoderm**, on one side. The yolk is arranged in such a way that near the nucleus a dense mass is left out. This is the **yolk nucleus**, which as it grows in size is called **latebra**. The latebra of the mature oocyte is of light yellowish appearance. Its yolk is called **white yolk**, a darker **yellow yolk** develops later. As the oocyte increases in size the latebra becomes centrally located and is surrounded by alternating concentric thin layers of white and thick layers of yellow yolk. Finally, the centrally located nucleus of the oocyte moves outward towards the periphery where it spreads out to form a whitish disc, the **nucleus of Pander**. Its passage to this position is marked by a narrow strand of white yolk, the **neck of latebra**, extending from the latebra to the surface of the egg. The nucleus of Pander is a small white spot visible on the "yolk" of chick egg. On its surface, embedded in its white yolk is a microscopic mass of active cytoplasm, the **germinal spot**, containing the nucleus, the **germinal vesicle**. The germinal vesicle is large in the beginning but becomes reduced after maturation.

It requires twenty-one days of incubation before the young chick is ready to hatch, and during this time these structures within the egg form practically the whole of its world. All the embryo required from outside is oxygen, warmth and from time to time a rotation or turning of the egg. The oxygen is obtained through the shell. It is absorbed by the membrane of the yolk-sac and distributed to all parts of the body. Energy is derived mainly from the oxidation of carbohydrates and fats. Warmth is derived from the body of the mother during incubation. As there is considerable amount of temperature difference¹ between the side of the egg in contact with the hen's

¹According to Burke (1925) the temperature difference of as much as 8°C may exist between the top and bottom of the egg.

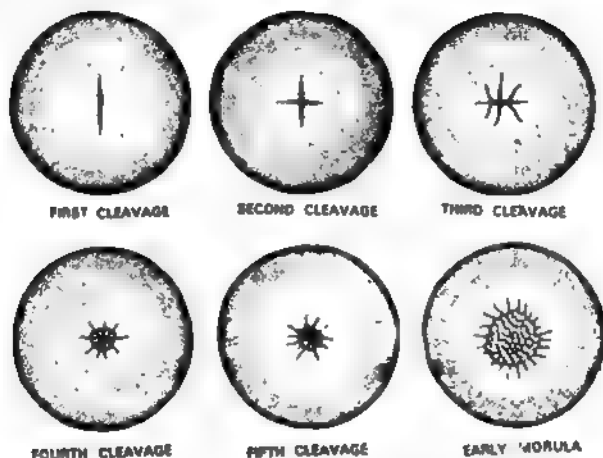


Fig. 7.48. Cleavage of the egg of hen.

nucleus. Both unite. The union of the gametic nuclei restores the diploid number of the chromosomes typical of the species.

Cleavage. Shortly after the union of the gametic nuclei (fertilization) the **zygote nucleus** prepares for segmentation, as such, it is called **segmentation nucleus**. Usually the process of fertilization, it is believed, completes with the formation of the **first segmentation spindle**.¹ The fertilized egg is morphologically a single cell with a single segmentation nucleus. Most conspicuous part of the early development is cell division or cleavage, as such this period is called the **cleavage or segmentation period**. The first cleavage appears in surface view as a narrow furrow extending across the central part of the blastodisc (Fig. 7.48). This appears about three hours after fertilization. About twenty minutes later the second division begins, although the first is not yet complete, the ends of the furrow keep on extending. Cleavage begins with a vertical division in two cells and the two furrows (of second division) meet the first cleavage furrow at right angles. These two meet in such a way as to form a straight line (in some cases these two furrows may meet the first cleavage furrow at separate points, in which case the intervening part of the first furrow becomes bent at an angle forming a cross furrow). The third cleavage planes are also vertical but they tend to be variable.

These cleavages do not form complete cells. What they form are protoplasmic areas with separate nuclei (marked out by cleavage furrows) in a continuous mass of protoplasm. The furrows do not cut through the entire depth of the blastodisc, the lower layer of the protoplasm being continuous. The furrows do not extend in the marginal zone of the blastodisc (periblast). Thus at their margins all the cells are connected by the unsegmented ring of periblast. Such a partial cleavage is called **meroblastic** in contra-distinction to the complete (**holoblastic**) cleavage. Besides this, some observers have pointed out that the centre of the cleavage (i.e., the place where the first cleavage furrows cross) is sometimes excentric, this displacement being towards the posterior end of the blastoderm. This, however, is not a normal feature, it may or may not occur.

After the third cleavage the egg moves down into the uterus and within next four hours progresses from eight to approximately 256 cell stage. The later cleavage furrows are irregular, but in surface view two types of furrows may be noted: (i) those that cut off the inner ends of the cells, and (ii) those that run radially. The furrows of

¹ For all mitotic divisions a protoplasmic spindle is formed.

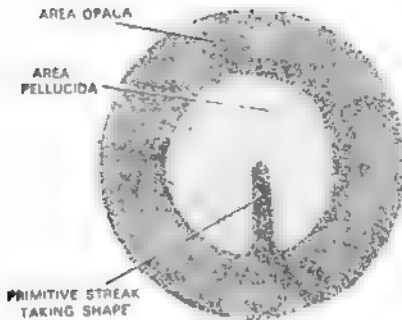


Fig. 7.51. Surface view of the blastoderm at the end of cleavage showing formation of primitive streak.

from the observer. This rule is subject to a great variation as noted by its discoverer von Baer.

Gastrulation. In *Amphioxus* and frog the formative movements of gastrulation result in the enclosure of the endoderm and mesoderm within the ectoderm and the laying down of the main axial structures of the embryo. Normally all these processes are accurately geared with one another and go on together at one and the same time. Here the process of gastrulation has departed considerably from the pattern of other chordates because of the presence of large amount of yolk. In the chick process of gastrulation is separable into three distinct phases, namely, the **laying down of the embryonic endoderm**, **mesoderm formation** and the **formation of the embryonic axial structures**.

Before considering the process of gastrulation it is better to understand certain regional differentiations that take place at the time of gastrulation. The outermost cells of area opaca grow so rapidly that they become partially lifted up from the yolk forming the **margin of overgrowth**. Adjoining this outermost layer the cells of the area opaca still adhere to and are continuous with the yolk from which new cells are continually formed. This ring-like region is considerably wider than the margin of overgrowth and is known as **zone of junction**. As the blastoderm increases in size the zone of junction is necessarily pushed further outward, thus, releasing cells for the increase of the area pellucida. These free cells, just lifted off from the yolk at the inner margin of the zone of junction, constitute the **germ wall**.

Before gastrulation begins the roof of the blastula is three to four cells thick. But with the beginning of gastrulation the roof thins out on one side and becomes one or two cells (Fig. 7.48C). Eventually the blastoderm, in this region, becomes free from the underlying yolk and forms a small slit-like opening into the blastocoel. This opening is the **blastopore**, but not the entire blastopore (as compared to the blastopore of *Amphioxus* or frog). The elevated cells are homologous to the **dorsal lip** of the blastopore. In the chick gastrula it is physically impossible to form a ventral lip by epiboly (as in the frog) on account of the large amount of yolk. The cells of the dorsal lip soon begin to involute into the blastocoel, thus forming the **mesentoderm**, which later on forms the endoderm and mesoderm. Because in the earlier stages separate germ layers ecto-, ento-, and mesoderm are not formed. Some investigators have now started using the old term **epiblast** and **hypoblast** to designate the undifferentiated layers. The term epiblast is used for the outermost layer of cells of blastodisc and hypoblast for the lower one. This non-committal nomenclature is retained until the separation of the mesoderm from either of them has taken place. The cells of the hypoblast (mesentoderm) are delaminated or budded off from the under surface of the blastodermal layer (epiblast).

Endoderm Formation. At gastrulation when the blastoderm is turned inward into

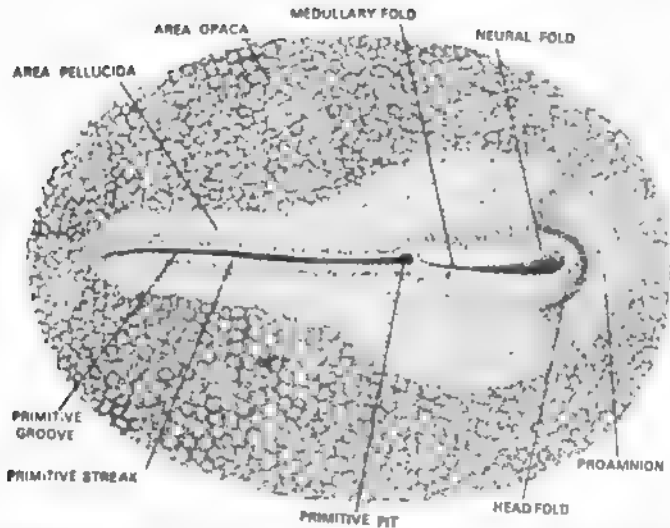


Fig. 7.53. Total view of the dorso-lateral aspect of chick embryo showing the formation of the head fold (19 hours' incubation).

cells is slow, the streak formation also takes place gradually. First a short broad initial streak appears as a conical thickening almost as broad as long about six to seven hours after incubation. This is rather a transitory stage and soon it extends from the posterior margin to approximately the centre of the pellucid area. The streak is relatively broad and reaches its maximum length in about 18 to 19 hours. Soon a swelling of cells appears at the anterior end of the streak and is called the **primitive knot** or **Hensen's node**. It is formed of cells from the prospective notochordal area and those that will form the floor of the neural tube. By this time the area pellucida stretches in an antero-posterior direction, it loses its circular shape and acquires a pear-shaped outline, the blunt end being anterior. The streak extends over two-thirds to three-fourths of its length and is just like a thickening in the beginning. Later it acquires a groove, the **primitive groove**, along its length. The pit appears because the rate at which the mesodermal cells leave its lower lateral borders is greater than the rate at which the streak is renewed from the upper-layer cells along its upper border. The primitive groove is flanked on both sides by **primitive ridge**. Posteriorly it ends in a **primitive plate** and anteriorly in the **primitive pit** (Fig. 7.53).

The primitive streak, it is apparent, is formed because of crowding of the notochordal and mesodermal cells towards the mid-line. The mesodermal cells on reaching the streak do not stop there, they pass inwards and then leave the sides of the streak and migrate out laterally to form a sheet of cells on each side between the endoderm and the upper layer of cells. Later (about 19-22 hours of incubation) some of the cells take a more anterior course to form two forwardly directed horns to the sheets of mesoderm. The cells of the primitive knot migrate in a forward direction only so as to form a column of cells the **notochord** or **head process**. The head process, as such, is visible as a rod of condensed mesoderm extending forward from the anterior end of the Hensen's node (Fig. 7.52A). It lies in the mid-line below the prospective neural plate whose middle part (or floor plate) is formed by cells lying in the upper part of the primitive knot.

After the primitive streak the region around and anterior to it becomes opaque, with the result that the transparent area pellucida now contains a darker central region (the

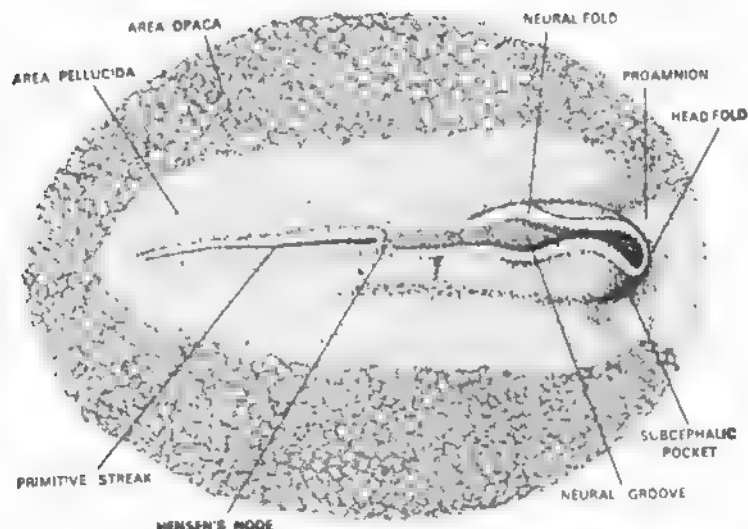


Fig. 7.54. The total view of the dorso-lateral aspect of the chick embryo (21-hours) Head fold growing, primitive streak diminishing and first interomitic furrow indicated in front of Hensen's node.

embryonal area) that is destined to give rise to the embryo proper. The blastoderm extending beyond the limits of this area (extraembryonal area) gives rise to accessory embryonic organs that are discarded at hatching. The formation of the embryonal area is indicated by a thickening of the median strip of ectoderm anterior to the Hensen's node. This is the **neural plate**. Soon the margins of neural plate become elevated forming the **neural** or **medullary folds**. The neural folds extend from the anterior lateral sides of the primitive streak forward, and at the anterior border of the neural plate they unite with each other. Thus with the formation of the neural folds the neural plate becomes grooved longitudinally, the groove being called the **medullary groove**.

Simultaneous with the formation of the neural folds the entire thickness of the blastoderm at the anterior region of the neural plate becomes elevated. Consequently a process is formed which juts forward over the underlying ectoderm. This is **head fold**, that differentiates into the head and anterior region of the embryo as the development proceeds further. Under the elevated head a pocket-like recess is formed like a shallow trough beneath the head. This is called the **subcephalic pocket** (Fig. 7.55).

In the formation of the head fold the entire thickness of the blastoderm is involved as such along with it the underlying endoderm also becomes elevated, and is pushed into the head-fold forming a shallow pocket. Thus, a small saccular part having an edodermal lining on all sides is cut off from the large general archenteron. This portion is called the **fore-gut** and its opening into the archenteron is called the **anterior intestinal portal**. The remaining portion of the archenteron is now onward called **open mid-gut** and **hind-gut**. In later development (60-72 hours of incubation) the hind-gut will be constricted off in a similar way in the formation of the tail region.

Gastrulation of Chick, *Amphioxus* and frog. Although there is no apparent similarity between the process of gastrulation in the chick, *Amphioxus* and the frog, a closer examination reveals that the process is similar basically, whatever differences there are, occur because of the extremely telolecithal condition of the egg. As in other

animals gastrulation consists of formative cell-movements. A separate layer of endoderm is formed before mesoderm production begins because a yolk-digesting layer is needed, as in the chick yolk is much abundant and cannot be enclosed within the cells of the embryo as in *Amphioxus* or the frog in which yolk is enclosed during cleavage within blastomeres.

In the chick gastrulation, at an early stage, when the blastoderm occupies a small area on the top of the yolk, gastrulation by invagination is not possible, and an archenteron (as in others) is not formed. On the other hand, a separate sheet of endoderm is segregated early and the notochordal and mesodermal cells pass inwards through the primitive streak, a structure which is not formed in other lower forms. The primitive streak (along with its primitive knot) is the place at which mesoderm and notochordal material migrate below the superficial layers. Similar function is performed by the dorsal and lateral lips of the amphibian blastopore. These structures can be considered to be comparable. For this reason some authors in the past called the primitive streak is homologue of "fused lips of the blastopore". But this is not

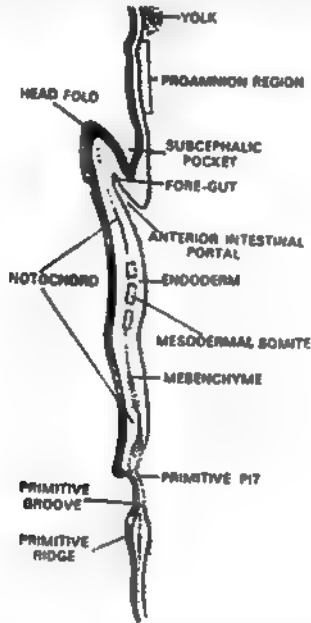


Fig. 7.55. A longitudinal section of 24-hour chick embryo.

correct. The primitive streak is not connected with the formation of the archenteron or its equivalent and as a result of its activity no true blastopore is formed. It is, therefore, better to consider this as a new structure evolved to meet the needs of a gastrulation of materials spread out in a single layered blastoderm.

In the frog's blastula there is a tendency of the ectoderm to spread in all directions so that the yolk becomes enclosed from all sides. This is not possible in the chick. But for this difference the general layout of the areas of prospective epidermis, neural plate, notochord and mesoderm on the blastoderm is similar to that on the surface of the frog's blastula. The formative movements of the main embryonic area in both are

similar. There is a **convergence** of the material towards the mid-line, there is a **migration** inwards and forwards (of notochordal and mesodermal material) and **extension** in the longitudinal axis of the embryo. All this leads to the conclusion that the process of gastrulation in the chick, in the frog and in *Amphioxus* is fundamentally similar. Strictly speaking a "gastrula" (embryo with two primary germ layers, ectoderm and endoderm) in the older sense does not occur in any of the three types.

Later Development

Towards the close of gastrulation the main features of the embryo include: (i) the **notochord** (or notochordal process) formed independently (unlike the frog) from undifferentiated cells between the two advancing mesodermal sheets but by proliferation of cells anteriorly from the undifferentiated area of Hensen's node; (ii) the **neural plate cells**, in the upper layer of the embryonal area, which have converged in the mid-line forming the rudiment of the central nervous system, and the remaining cells of the upper layer from the epidermis; and (iii) an indication of the formation of the head fold

Mesoderm. At the early head fold stage the lateral sheets of mesoderm spread from the sides of the notochord and laterally across the area pellucida. The inner margin of each sheet becomes thickened to form a distinct band of cells bordering the notochord on either side. This is the **paraxial mesoderm**. The paraxial mesodermal sheet forms

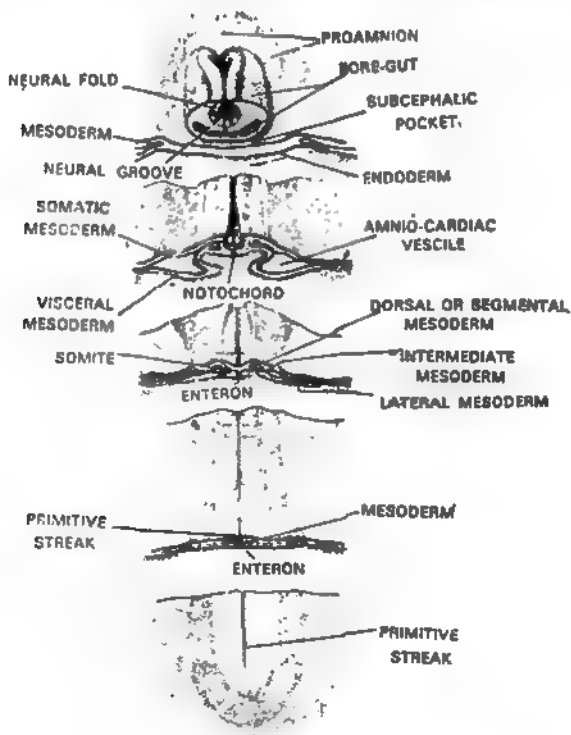


Fig. 7.56. Serial transverse sections of 24-hour chick.

the lateral plate. These two are connected by the non-segmented intermediate mesoderm. The outlying mesoderm become segmented by transverse grooves (*intersomitic furrows*) leading to the formation of somites. As the development proceeds the number of somites increases. The first pair of somite is separated in front of the primitive knot. As further pairs of somites appear the primitive streak shortens. The somites are the most important indicator of development stages. Chick embryos having the same number of somites are approximately at identical stages of development. It is possible to compute the age of chick by knowing the number of somites. The first pair of somites appears in about 21 hours incubation, the 24-hour chick has four somites, the 33-hour chick has thirteen, and the 44-hour chick has twenty-four. Though not very accurate this method of computation is quite helpful in the studies of embryology. In the later stages of development each trunk and neck somite differentiates into a *myotome*, *sclerotome* and *dermatome*. The myotome finally gives rise to voluntary muscles, the sclerotome develops into vertebrae and connective tissue and dermatome is transformed into dermal layer of the skin. By the time of 50 to 53 hours of incubation twenty-two pairs of somites are formed. Beyond this period the number of somites becomes increasingly difficult to determine with accuracy. First the lateral sheets of mesoderm extend nearly to the margins of the blastoderm later they grow forwards and fuse in front of the notochordal process, but a small area ("proamniun") below the head fold is still, for a time, free from mesoderm.

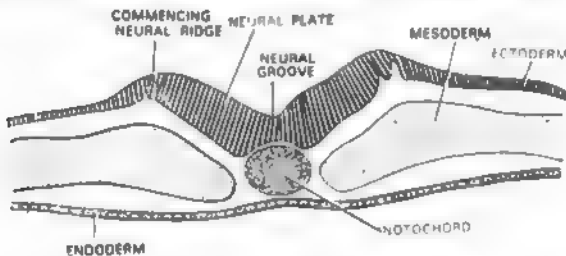


Fig. 7.57. Transverse section across the embryo at the twenty-fourth hour of incubation.

After 26 to 29 hours of incubation four pairs of somites are produced. By this time certain mesodermal masses of cells called **blood-islands** are also established in the posterior half of blastoderm. The cells occupying the inside of each blood island form **blood corpuscles** while the cells on the outside form a wall surrounding the corpuscles. Soon the blood islands run together forming a plexus of small blood vessels in the central part of the area opaca, now called **area vasculosa**. To differentiate from this the peripheral zone of the area opaca into which mesoderm has not yet penetrated is called **area vitellina**.

The mesodermal somites appear as blocks of cells containing a transitory cavity known as **myocoel**. From the developmental point of view the somites are important structures as they give rise to several fundamental organic differentiations. The intermediate mesoderm connects the dorsal with the lateral mesoderm and is itself unsegmented although it gives rise to segmental **nephrotomes**, that later gives rise to segmental nephric (kidney) tubules forming the **mesonephros**.

The lateral mesoderm is also unsegmented, but soon in its interior small clefts and spaces appear between the cells. These run together to form a cavity enclosed between the newly formed two layers of the mesoderm. The cavity is known as the **coelom**, the upper layer of mesoderm (next to the ectoderm) is the **somatic layer** and the lower layer (next to the endoderm) is the **splanchnic layer**. The two sheets of the lateral mesoderm extend from the embryo far out into the extraembryonal area as such the coelom also extends into that area. The portion of the coelom in the embryonal region is the **embryonic coelom** or **splanchnocoel** and that in the extra-embryonal region is

the extraembryonic system. With the appearance of the coelom the ectoderm together with its somatic layer of lateral plate mesoderm, then becomes known as **somatopleure**, and the endoderm with the layer of splanchnic lateral plate mesoderm together form the **splanchnopleure**.

Main Embryonic Organs. By 24-hour incubation almost all these changes take place. Following this stage rudiments of many of the main organs make their appearance

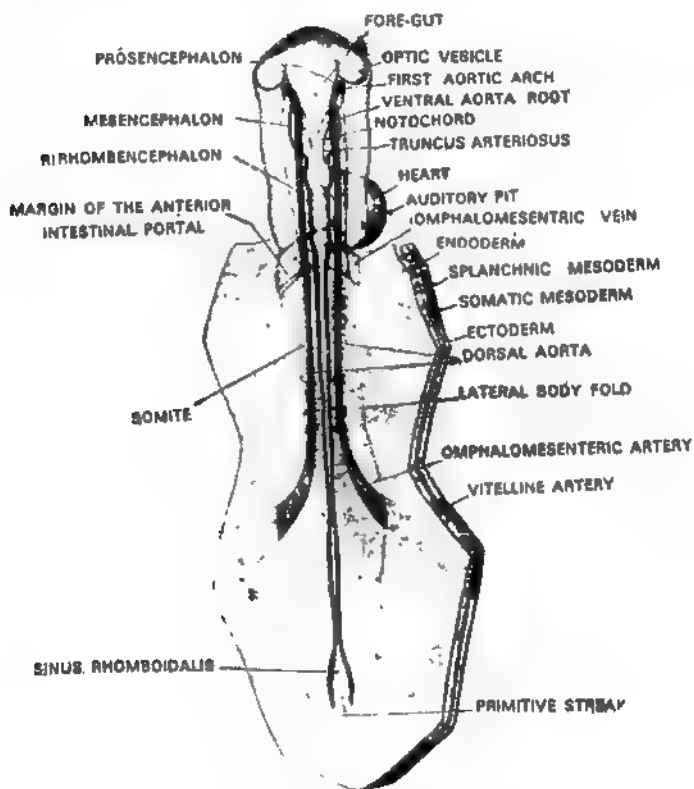


Fig. 7.58. Dorsal view of 33-hour embryo of chick.

Central Nervous System. Soon the neural folds unite dorsally and proceeding with their fusion forward as well as backward, form the neural tube. The neural folds do not close simultaneously throughout their length. After about 26 hours incubation (four somite stage) the neural folds first meet at the level of mid-brain and the fusion continues both ways. Anteriorly the fusion is delayed for a few hours and an opening at the tip persists for some time. This is the **anterior neuropore**, which closes eventually leaving a scar visible in later stages (say 33-hour chick). The fusion of the neural folds posteriorly is delayed much and the opening left out on that side is the **posterior neuropore**. A careful examination of the embryo at this stage reveals that behind the last mesodermal somite the two neural folds diverge (Fig. 7.49) and after havin

passed the ever-shortening primitive streak they gradually fade into the superficial ectoderm. Thus the posteriorly diminishing neural folds enclose a shallow area called **sinus rhomboidalis**. This is actually the posterior part of the neural plate which will finally form the complete neural tube.

Each neural fold consists of a superficial (**non-nervous**) and a deeper many layered (**nervous**) ectoderm. During fusion only the superficial ectoderm unites over the neural tube while the nervous layer sinks into the tissue. When the two neural folds unite dorsally some loose cells appear between the ectodermal component of each fold. These cells form two bands, one on either side of the dorsal aspect of the tube. These are the **neural crests** which later become segmented by the disappearance of cells in the intersegmental positions. They form the dorsal root ganglia of the spinal and the cranial nerves as well as ganglia of the autonomic nervous system. They first appear in the anterior region of the embryo and are gradually added posteriorly as the embryo grows.

The neural folds in the head region present a metameric structure before fusion. The segments are called **neuromeres** but are very vague. At least eleven neuromeres have been recognised. Whether it is the total number for the entire brain is not known. Soon after the completion of the neural tube, on the anterior side three **primary cerebral vesicles**, typical of the vertebrate brain, are formed. These include the **fore-brain** (prosencephalon) comprising first three neuromeres, the **mid-brain** (mesencephalon) including next two neuromeres and the **hind-brain** (rhombencephalon) consisting of the remaining six neuromeres. As soon as the three cerebral vesicles are separated the neuromeric constrictions of the first two parts disappear except those separating these vesicles. The neuromeres of the hind-brain persist for about three days. Before long the fore-brain gives rise to sac-like lateral outgrowths called the **optic vesicles**. They begin their appearance after about 29-hours' incubation and in the 33-hour chick they are the most conspicuous differentiations of the entire brain.

Notochord. In the beginning the notochordal process is a rod of more or less undifferentiated cells, but it becomes more compact in form as the development proceeds. This is the **notochord**, that soon acquires a sheath of mesenchyme cells derived from the sclerotomes. These cells and their descendants give rise to skeletogenous tissue in which the vertebrae are laid down.

Enteron. Up to now the fore-gut is the only portion that is formed during the formation of the head fold. It is a blind tube, opening posteriorly at the anterior intestinal portal. The foregut increases in length continually as the fusion of right and left sheets of splanchnopleure progresses. By the time about 12 somites have been delimited (about 40 hours incubation) the posterior margin of the head fold has grown as far back as the posterior end of the hind brain. The part of the foregut formed at this stage is very broad and will give rise to pharynx. On its anterior face the endoderm fuses with the ectoderm to form the oral plate. This is the place where a perforation will appear to place the pharynx in communication with the stomodaeum. Then along the side walls of the pharynx four evaginations appear on each side. These are the **pharyngeal pouches**. The lips of these finally fuse with the ectoderm. The first three of these pouches break through or perforate forming the visceral clefts, but the fourth does not perforate at all.

The **mid-gut** is very characteristic. It does not have a cellular floor. Such a gut is called open gut. It begins at the anterior intestinal portal where it has well-defined lateral walls which diminish in size and tend to flatten out to become continuous with the roof of the open gut as one proceeds posteriorly towards the hind-gut. The lateral margins of the closed foregut continue as the lateral folds of the mid-gut. They tug the lateral walls inward toward the mid-line thus suggesting that the future midgut will completely constrict off from the underlying yolk. The gut is not completed as a continuous tube until the yolk is totally enclosed in the yolk sac, which then appears as a bag-like appendage of the gut to which it remains connected by a hollow stalk, the **yolk sac stalk**.

The hind-gut appears quite late, after about forty-five hours of incubation. It begins its appearance without the external appearance of a tail fold. Only a faint posterior swelling, the **tail-bud**, is visible containing within its tissue the sac-like hind-gut which

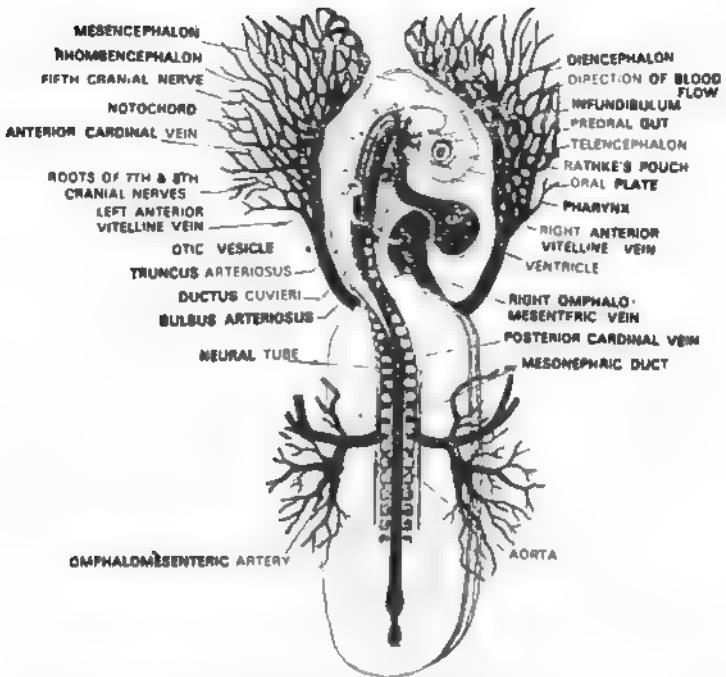


Fig. 7.60. Dorsal view of 48-hour chick embryo.

opens into the mid-gut through the **posterior intestinal portal**. The tail-fold faces toward the anterior side. At the most posterior portion of the hind-gut, the endoderm comes in direct contact with the superficial ectoderm forming the **anal plate** which perforates, finally opening into the **proctodaeum**, an ectodermal invagination that develops later. This region represents the posterior portion of the former primitive streak. The anal plate is directed dorsally in the beginning but with the development of the tail-bud the anal plate is carried ventral-ward.

Heart In the 24th-hour chick a thickening of splanchnic mesoderm appears near and posterior to the anterior portion intestinal portal (Fig. 7.61). Within next three hour this thickened mesodermal portion buds off cells into the narrow space between itself and the endoderm. It is just where the lateral plate-mesoderm from both sides is approaching to form the pharynx. The right and left coelomic cavities here become very large and are usually referred to as **amniocardiac vesicles** because of subsequent fate. The cells budded off are destined to form the **endocardium** of the heart, and are organised early into short tubes with walls only one-cell thick. These tubes are surrounded by thickened splanchnic mesoderm known as the **epimyocardium**. As mentioned above the anterior intestinal portal is being pushed more posteriorly. As this happens the endocardial tubes with their epimyocardial envelopes approach each other and fuse beneath the newly formed fore-gut. Consequently a single double-walled tube is formed. This is the embryonic heart. This tube is held in place by dorsal and ventral **mesocardium**. The ventral mesocardium disappears soon after it is formed, while the dorsal mesocardium persists for a few hours more, disappearing eventually except near the sinus venosus, where the tubular heart begins to dilate and twist upon itself. The epimyocardium gives rise to thinner outer **epicardium** and the

it dilates and bends on itself. As it begins to elongate anteriorly it gives rise to two ventral aortic roots (**mandibular arteries**) and posteriorly it receives the two **omphalomesenteric veins**. When the cardiac tube elongates, it bends upon itself since it can neither push forwards nor backwards. It naturally forms a loop which is S-shaped. With further growth it becomes separated into four chambers by transverse constrictions. The **sinus venosus** and **atrium** develop at the junction of the two omphalomesenteric veins. Further flexure of the heart towards the right forms the **ventricle**; at the anterior end where the two ventral aortic roots leave the heart is the **bulbus cordis**.

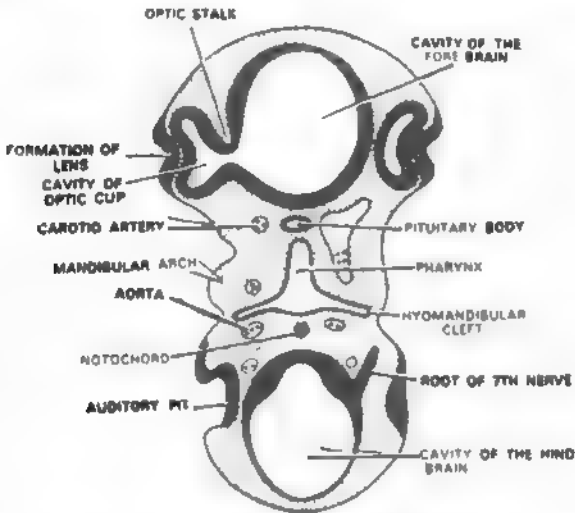


Fig. 7.63. Transverse section of the head of 48-hour chick embryo.

Embryonic Blood Vessels. In the area vasculosa of the embryo the blood vessels arise very early during development. They are formed even before any somites are visible. By the time the first somite is cut off, small vessels appear in the area pellucida. They are in continuity with those of the area vasculosa. At this stage it appears that the vascular network of the area vasculosa gradually encroaches on the area pellucida. By the time seven somites are delimited, vessels begin appearing in the lateral plate mesoderm of the embryo itself. The embryonic vessels are all of small calibre in the beginning and follow on set plan, but later, those in particular region enlarge so as to conform to a definite pattern and an orderly circulation is established in the embryo. This differentiation takes place rather rapidly and accompanies the formation of a definite system in the extraembryonic area with the result that a complete circulation is established throughout the entire blastoderm. In the 33-hour chick a circular peripheral vessel, the **sinus terminalis**, is differentiated. This surrounds the area vasculosa around its entire boundary. Many centrally placed network open into the sinus terminalis through small vessels, along its whole length. A pair of large veins, the **anterior vitelline veins**, connect the sinus terminalis directly with the embryo. Each of these veins passes backwards along the inner margin of the area vasculosa and then at the level of the heart is connected with the embryo by a transversely running vessel, the main **vitelline vein**, which fuses with its fellow of the opposite side to form a short but large vessel, the **ductus venosus**, which empties in the sinus venosus.

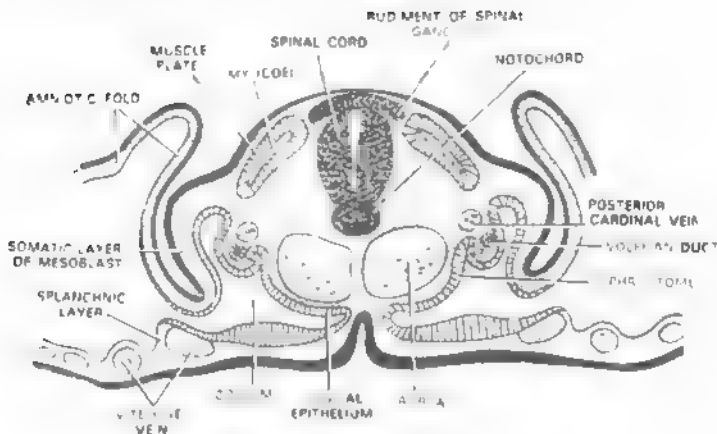


Fig. 7.65. Transverse section of 48-hour chick embryo across the body

in a manner similar to the amniotic head fold. During the fourth day of incubation the two folds, advancing towards each other, meet and fuse with each other at a point about a quarter of the way from the posterior end of the embryo. The place of the two folds is marked by a scar the **seroamniotic connection** (Fig. 7.67).

The amniotic folds are formed from somatopleure which is composed of ectoderm and somatic mesoderm. Since a fold is formed as a result of reduplication of the somatopleure, two separate layers are formed by the union of the amniotic folds, an inner and an outer one. The inner one is the **amnion** and the outer one **chorion**. In the amnion the arrangement of layers is reverse since it is formed by the fusion of the inner layer of the folds, the ectoderm is towards the inner side and the mesoderm towards the outer side. The chorion represents the outer half of the amniotic folds as such has the ectoderm on the outside and mesoderm on the inside. Between the two layers, the amnion and chorion there lies the **chorio-amniotic cavity** or **extra-embryonic coelom**,

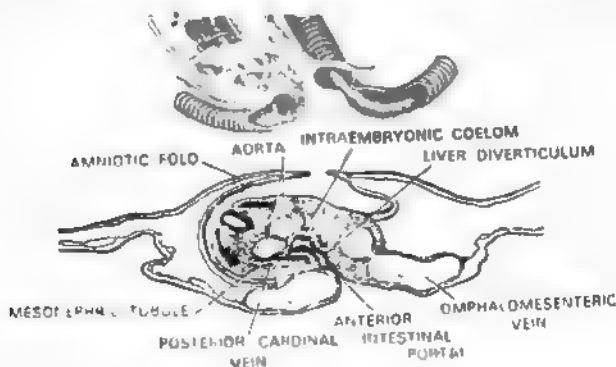


Fig. 7.66. Section through the anterior intestinal portal of the 48-hour embryo of chick.

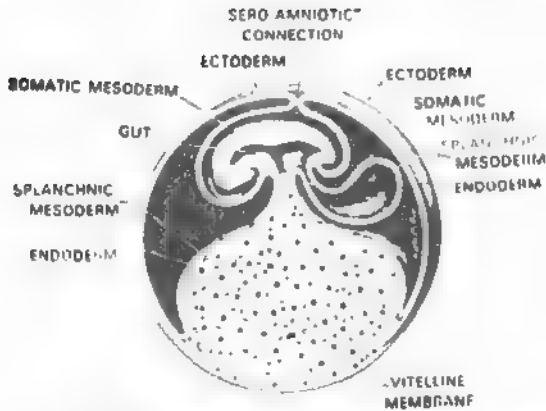


Fig. 7.67. Formation of embryonic membranes in the early embryo of the chick.

which is in direct communication with the coelom inside the embryo (**intraembryonic coelom**). The chorion grows around the yolk sac enveloping it completely at the end of the second week. It expands and adheres to the entire calcareous shell membrane, so that the embryo with all its foetal membranes within the shell is surrounded by it.

Allantois. The hind-gut is formed by the tail-fold of the embryo before the embryo is of about 28 somites. Soon after its formation, the ventral wall of the hind-gut, just in front of the anal plate, grows out to form a sort of bud which projects out into the coelom. This bud is **allantois**. Being an outgrowth of the gut, the allantois is composed of splanchnopleure, that is an inner layer of endoderm and an outer layer of splanchnic mesoderm. It grows out rapidly and invades the extraembryonic coelom as early as fourth day of incubation. It is filled with a saline liquid, imparting to it a bag-like shape in embryos of five to six days of incubation. Its distal portion is called the **allantoic vesicle** and gradually replaces the extraembryonic coelom (**sero-amniotic space**), wedging itself between the amnion and chorion. The proximal (intraembryonic) portion of the allantois is called the **allantoic stalk** (which in mammals forms the urinary bladder). Upon attaining its full size the allantois replaces the entire extraembryonic coelom and extends itself around the entire embryo, and its

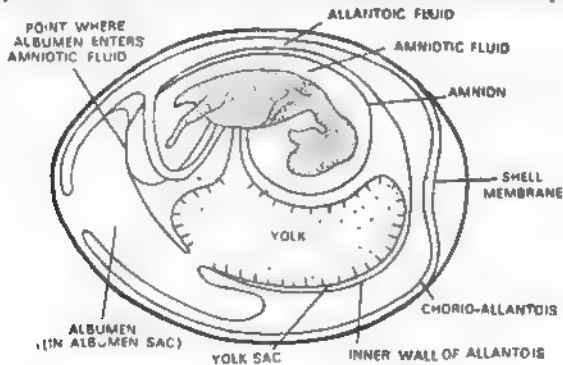


Fig. 7.68. Embryonic membranes of the chick

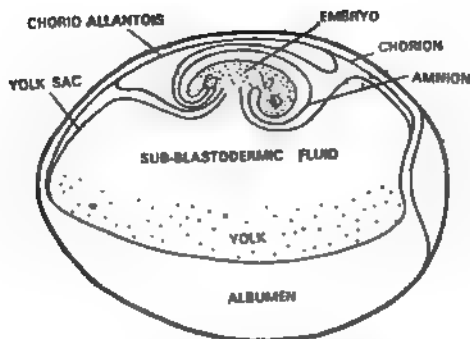


Fig. 7.70. Yolk sac.

enteron in the earliest chick embryos and forming the complete fore-gut and hind-gut is the same cellular layer that covers the yolk-sac. As the yolk-sac diminishes in size, the splanchnopleure follows the yolk-sac into the embryo, where it forms the lining of the midgut. This suggests that the yolk-sac is really a part of the gut (as in the frog embryo). Eventually it is incorporated into the small intestine of the chick, where it persists for several days after hatching.

The yolk is used directly as food by the early embryo. The endoderm lining the yolk sac is specialised both to digest the yolk and to absorb the product of digestion. To increase this surface the wall of the yolk-sac becomes folded and three folds dip down into the yolk forming the so-called *yolk-sac septa*. The yolk is broken down into diffusible substances, digested by enzymes from the ectoderm of the yolk-sac and picked up by the capillaries in the area *vasculosa*. These capillaries through the *vitelline veins* send blood to the heart, which propels it to all parts of the embryo and to extraembryonic tissues and organs. The blood is carried away from the heart through *vitelline arteries*. As the yolk stalk is formed the vitelline veins and arteries are brought together.

The formation of the chief embryonic organs has been given. Here the formation of some other important structures, not mentioned above, is given.

Optic Vesicles. In neurosensory system the *optic vesicles* make their appearance after 33 hours incubation (in 10-somite stage), after about forty hours incubation they are constricted at the bases, about five hours later the optic stalk is established and the optic cup is completely formed between 40 to 55 hours' incubation. Further stages in the formation of the eye follow soon.

Auditory Sacs. The first indication of the formation of the *auditory sacs* is met with at the 12-somite stage. They appear in the form of circular patches of thickened ectoderm on the dorsal surface of the head opposite the posteriormost neuromeres of the hind-brain. The auditory placode is slightly depressed at the 14-somite stage and it forms a wide open pit in the 16-somite stage. The pit narrows and closes by 20-somite stage thus forming the auditory sac or vesicle. Further, stages are similar to ear formation in other vertebrates.

Olfactory Pits. The ectoderm of the side of the head, a short distance in front of the eyes, appears thickened to form two circular patches of ectoderm at about 28-somite stage. This is the first indication of the *olfactory epithelium*. Soon the *olfactory plates* sink into the dorsal portion of the head. By the time 36 somites appear each becomes a deep olfactory pit situated at the junction of the sides and ventral surface of the anterior portion of the head, with the wide mouth opening outwards and ventrally. Soon the olfactory epithelium becomes differentiated from the ectoderm.

Appendages of Alimentary Tract. *Stomodaeum.* At the 12-somite stage the oral plate is formed and lies in a slight depression on the under surface of the head. This

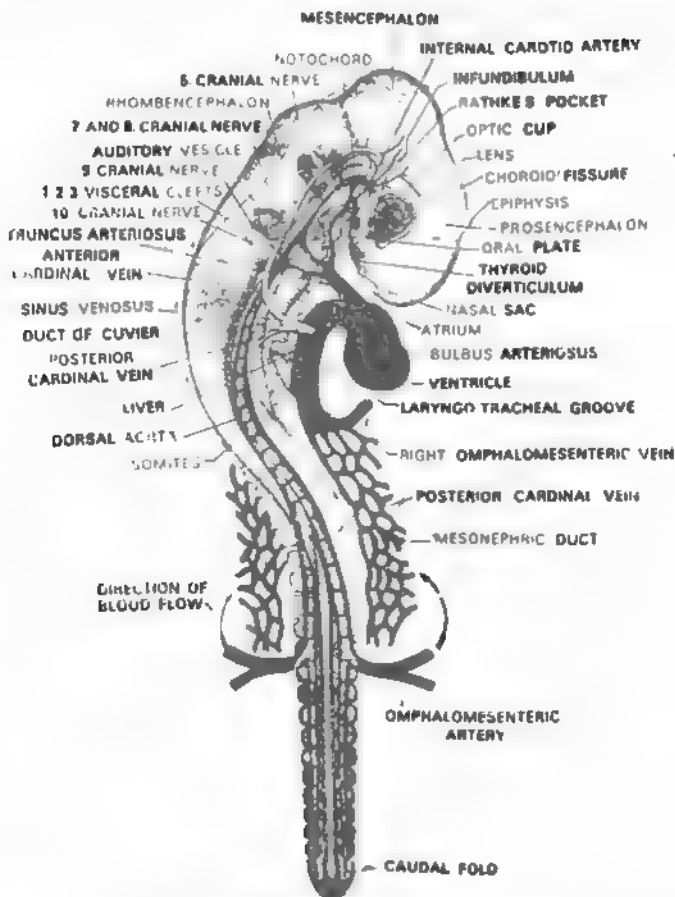


Fig. 7.76. 72-hour chick embryo, the amnion has been removed.

enlarges and forms the ectoderm lined **stomodaeum**. With the breaking of the oral plate it communicates with the foregut.

Pharynx The pharynx has been defined as the alimentary canal of the head. It is the most variable part of the alimentary canal of vertebrates. It is modified for respiration. In the aquatic vertebrates it bears visceral clefts and arches and in the terrestrial forms lung. During development, therefore, it first forms visceral clefts and arches and then gives rise to the air-breathing lungs. The extreme anterior end of the pharynx extends at first some distance in front of the oral plate (preoral gut) but after the rupture of the oral plate a laterally expanded tube is left. Soon furrows appear in the wall forming the visceral pouches ultimately. The pouches are formed by the branchial portion from which the ventral post-branchial portion of the pharynx is separated by lateral clefts. The larynx, trachea and lungs develop from the ventral division.

Liver. The liver arises as two diverticula of the endoderm of the anterior intestinal

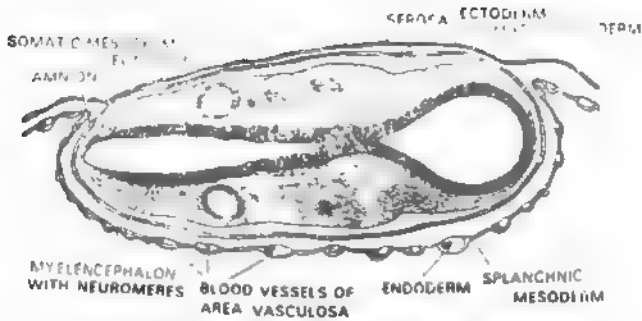


Fig. 7.72. Section through the auditory vesicle of the 72-hour chick-embryo.

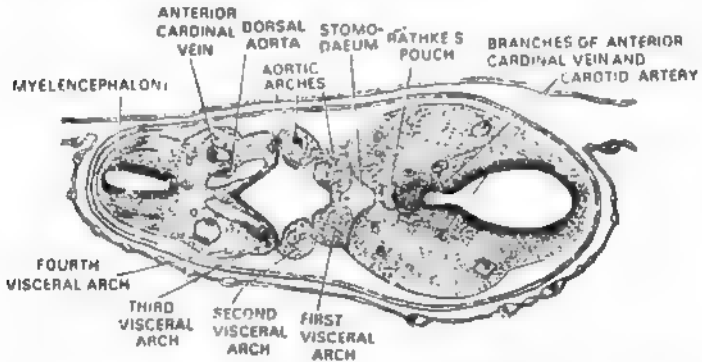


Fig. 7.73. Section through the aortic arches and the pharynx of the 72-hour embryo of chick

portal, one situated immediately above and the other below the posterior end of the ductus venosus. As the anterior intestinal portal retreats backwards the original dorsal liver diverticulum becomes anterior or cephalic and the ventral becomes posterior or caudal. These two form the left and right lobes of the liver by 30 somite stage.

Pancreas. The pancreas develops from a dorsal and a pair of ventral primordia. The dorsal diverticulum is an outgrowth of the dorsal wall of the intestine immediately above the posterior liver diverticulum. The ventral diverticula arise from the posterior liver diverticulum.

Proctodaeum. Behind the anal plate a depression appears and widens to form the proctodaeum. With the breaking of the anal plate it opens into the hind-gut.

Lung. In the posterior part of the pharynx, where it merges into the oesophagus, another depression is formed in the centre of the floor, called the **laryngotracheal groove**. At first it is very narrow, but it soon deepens becoming sac-like and as it pushes away from the pharynx it forms an elongate diverticulum, divided into two lobes at its distal end. This is the pulmonary apparatus consisting, in this early condition, of an embryonic larynx, trachea and lung buds. The laryngotracheal groove appears soon after the second day of incubation and in 72-hour chick the two lung buds are well differentiated. The opening leading from the pharynx into the newly formed larynx is the glottis.

back and meet to form the hollow **pronephric duct**, which continues behind upto 33rd somite. It is never functional. The duct is hollow because it receives the hollow mesonephric tubules. The **mesonephros** develops before the pronephros has disappeared. In fact it encroaches upon the latter, by forming mesonephric tubules from the thirteenth to thirtieth somite. They develop glomeruli and become functional. Finally develops the **metanephros** or the adult kidney. It begins developing while mesonephros is still functional, but is fully formed at the time of hatching so that the young chick is equipped with a functional metanephros.

Gonads. The first indication of the presence of sexual development can be observed in the late 4-day chick. It is in the form of a slight swelling of the peritoneal epithelium, located between the mesonephros and the dorsal mesentery. This swelling is known as the genital ridge, is covered by epithelial cells (**germinal epithelium**) and contains mesenchyme cells, and primordial germ cells which are conspicuous by their larger size. These germ cells are found in the germ wall of the blastodisc at the late primitive streak stage. They remain there until the blood circulation has been established, when they enter the blood stream to be transported to all over the body of the embryo. Many of them are lost, but some finally arrive near the dorsal mesentery, where they leave the blood stream by amoeboid movement to take their place in the genital ridge. The development of tests and ovaries is similar.

GENERAL NOTES

Migration. The migration of birds is one of the most spectacular events in the animal world. It has intrigued mankind for centuries. Even now after more than 2000 years of observations climaxed by a century or more of experimental study many aspects of migration are not clearly understood. Migration has been defined as "a periodic passing from one place to another" (Cahn). Migrations are different from unidirectional movements and those in which animals are helplessly carried by some other agency. They are correlated with environmental periodicities or with some stage in the life history of the individual making the migration. Migrations may be (i) **daily** as of birds passing to and from a roost (crows, starlings or rocky herons); (ii) **lunar**, as in the case of marine organisms under the tidal influences; (iii) **seasonal**, including the regular as well as some of the irregular migrations of birds and (iv) **cyclic** movements correlated with some cyclic of longer duration than the seasons. Cycle and seasonal migrations are of great importance in bird life.

Most migrations are latitudinal, i.e. north and south. Birds move into the wide land masses of the north temperate and subarctic where there are facilities for feeding and nesting during the warmer months, and then retire south for the winter. In the Southern Hemisphere where the seasons are reversed a lesser and opposite migration occurs. Some birds perform altitudinal migrations into mountainous regions for the summer and return to the lowlands in winters. Such migration occurs in the Rocky Mountains and the Cascade Sierra Nevada systems of western North America.

Most migrants use established routes for migration and travel more or less on schedule, arriving and disappearing regularly "according to the calendar". Some birds migrate close to the earth and others up to 3,000 or 5,000 feet but rarely higher. The speed of the "migration front" averages about 25 miles per day, although individuals may fly at 30 to 50 miles per hour. The fall in the speed is because they stop to feed and are passed by others. Many species "follow the sun" and never experience the rigours of winter. With the help of singing or marking the birds it has been ascertained that many migrants return to places previously occupied by them. Both the summer and winter ranges of migrants are well defined.

Many theories have been advanced to explain the origin and perpetuation of the migratory habit in birds, but none of them is entirely adequate. Migration, presumably, is a phenomenon of multiple origin and no single factor or workable hypothesis can explain it. It has, however, been established that some migrants follow obvious landmarks, such as rivers, mountain ranges or coast lines, but there are many species that pass over the sea or lands without directional features. Evidently birds are guided by instinct impressed on the nervous system, in some way through countless

generations. It is further believed that the urge to migrate is related in part to the endocrines of the gonad. Further details of the phenomenon are beyond the scope of the present account.

Distribution Birds occupy all continents, the seas and most islands, penetrating the Arctic to beyond 80°N. and the Antarctic, and occur from sea-level to above timber line on mountains, even to above 20,000 feet on Mount Everest. Although the birds possess the power of flight yet each species occupies a definite geographic range and particular kind of habitat. In the Indian region (South of the Himalayas) Philippines and part of the East Indies there are seventy-eight families. The broad hills (Eurylaimidae, a rather primitive passerine family) are exclusively Oriental, but also occur in Africa. On the other hand, it shares 70 families (80.5 percent) with the Ethiopian region and 64 families (74.4 percent) with the Australian.

Activity and Food Being "warm-blooded" the birds are very active at all seasons. Diurnal species keep busy from dawn to dusk and owls and some others feed at night. Diurnal land birds sleep at night, with the head turned back on or beneath a wing. Water birds may sleep by day floating and dragging a foot to keep from drifting. The body temperature is regulated and usually above that of the environment. Because of their great activity they need large amount of food having high energy value. The fat storage of a bird is limited as such it cannot survive long without food. The birds "eat to live". Quail and other gallinaceous birds eat much leafy vegetation, but most species use concentrated materials such as seeds and fruits of plants. The many carnivorous species feed upon various animals including worms, arthropods, molluscs and vertebrates. There are many that eat only insects (flycatchers, warblers and vireos); many have fish as staple diet (loons, cormorants, pelicans, terns and king-fishers), herons eat frogs, some hawks capture both lizards and snakes; bird-hawks (sharp-shinned or duck-hawk) capture birds, many hawks and owls feed upon rodents and rabbits. Vultures feed upon dead animals (carion) and ravens and some hawks also feed upon dead animals. An adult bird may eat from a quarter to a half of their weight and nestlings eat relatively more, consuming as much as their own weight.

Enemies. There are a number of animals that destroy birds. The list includes the bird-hawks, a few owls, weasels, wild cats and foxes. Man is equally potential enemy of birds and "preys" on game-birds, often kills useful hawks and owls and at times, destroys birds that damage the crops. Many parasites, worms, protozoans, bacteria and viruses, attack birds, but their effects are poorly understood.

Reproduction. All birds lay eggs with much yolk and hard limy shell. Fertilization is always internal. For the development of the embryo eggs must be warmed or incubated for which either one or both parents sit upon the eggs. In some (chicken, quail ducks, shore-birds and others) the young chickens are well formed being fully covered with down feathers, and able to run about at once when hatched. Such young are called *precocial*. In many others (song birds, woodpeckers, pigeons, etc.) the young ones are *altricial*, i.e., they are blind, naked and helpless when hatched.

Most birds reproduce in definite seasons. The breeding activities are controlled by the endocrines, and follow increase in size of the gonads. The endocrines are perhaps effected indirectly by light. In certain experiments attempts were made to increase the length of the day by exposing the eggs to 40-watt electric light. This caused enlargement of the gonads, initiated song, mating behaviour and even egg production before time.

Courtship and display is a common feature among birds. Males of many species announce the advent of breeding season by uttering their characteristic songs at frequent intervals and many present a variety of courtship performances before the females.

Relation to Man Man's relation with birds began in prehistoric times. Long before man appeared on earth, the birds were well established and the number of flightless forms was far more than today. These birds could be easily captured, and man's first interest in birds was as a food supply. Earliest history records the use of birds as food. That way birds have helped man immeasurably. It is said that the penguins in the Antarctic saved a Dutch expedition from starvation en route to East Indies in 1599, the Cahow or Bermuda Petrel averted a famine in Bermuda in 1614. Many such

examples are available. Birds like dodos and elephant birds were exterminated primarily by navigators stopping off at Madagascar and nearby islands to replenish supplies.

Both wild as well as domestic birds are used as food. Among the wild birds there are the ducks, and geese, the fowl-like birds (quails, grouse, partridges, pheasants, turkeys, etc.) and shore-birds. The domestic fowl or chicken is extensively used as food and poultry raising forms an important industry. Special large bodied varieties are being raised these days. The turkey and guinea fowl are also valued for food and domesticated for the purpose although for raising these larger areas are needed. Peacock and certain Asiatic pheasants are considered delicacies. Domestic ducks and geese are also used for the purpose but the pigeons are in great demand in big cities.

The birds are of great value as sport. There are several varieties of game-birds such as the grouse, flocks of wild pigeons and the wild turkey that have attracted mankind in all parts of the world. Water fowl is another bird of great interest to bird hunters. There are many who have critical interest in water fowl hunting. Hunting ducks on the wing or on the water is a pleasure to accomplish and requires good knowledge and experience. But indiscriminate shooting of birds should be avoided, and it should be realised that there ought to be a closed season, if the species are to be preserved.

Bird Products. The eggs with their nourishing qualities form an important item of food. The domestic fowl is the chief source of eggs although those of ducks, wild fowls and pigeons are also used equally. The plumages of birds have served widespread use. From time immemorial feathers have been used for arrow-making for headgear and for ornamental wear. Down feathers from various species of waterfowls, ducks, geese and swans have been used since early times for clothing, bedding and stuffing pillows. The best quality of down comes from several species of eider ducks. In Arctic regions a number of legal eider down industries harvest the feathers of eiders on a large scale. In South America the skins of rheas are still used for rug making and their feathers extensively used for dusters.

In certain dry climates the unleached excrement (guano) of large colonies of fish-eating birds build up deposits which furnish an extremely valuable fertilizer, rich in phosphorus and nitrogen. Guano is one of great economic products (other than food). The most productive region is an island off the coast of Peru. The guanay cormorant (*Phalacrocorax bougainvillii*) has been called the most valuable bird of the world. At one time the revenue from guano deposits defrayed the entire cost of the Peruvian Government.

Birds are sometimes used for oil, though this is hardly practical for commercial purposes. In northern South America in caves along the sea coast the young of oil bird (*Steatornis caripensis*) are fed on rich fruit of palm trees till they become helpless globe of fat. They are collected by natives and fat is melted in earthen pots and used as butter. The oily bodies of small petrels are lighted to serve as torches. Oil extracted from penguins is used for candles in Antarctica.

Bird Friends. Birds are of great aesthetic value to man not only because of their bright colours and interesting ways but because of beautiful songs of many species. Many birds are kept as pets. Some birds of the hawk and owl family are rodent-eating. Hawks feed largely on small rodents, field mice, ground squirrels, etc. and owls are universal rodent destroyers. They seldom molest poultry as they are shy birds that avoid human habitations. Birds like finches and sparrows help to keep weeds in control. Sparrows generally eat all seeds of noxious weeds. Birds are very important insect destroyers. There is a wide variety of insect eating birds that keep the insect enemies of crops and fruits under control. Finally pigeons with their remarkably developed intelligence, sense of direction and power of undertaking long non-stop flights at high altitudes have been used as carriers of messages. Birds also aid dispersal of fruits and seeds.

Enemies of Man. Some species of birds are known to be definite enemies of man. Some such as sharp-shinned hawk, the Cooper's hawk, the chicken hawk, etc. depend on poultry and other birds for most of their food. They destroy earth worms and other useful animals. These are universally destructive. There are others that are seasonally destructive that feed on fruits, wild and cultivated fruits and seeds. There are some that

modern birds are included here. **Hesperornis* and **Ichthyornis* both possessed teeth and were aquatic. **Hesperornis* was a diver that had lost its power of flight.

Super order 2. Palaengnathae (Ratitae). Cretaceous to Recent. Flightless birds in which the sternum is without keel. Wings are reduced with long legs and curly feathers. Coracoid and scapula are nearly parallel. The palate is dromacognathus. The upper articular head of quadrate is undivided. Barbs of feathers are disconnected and barbules without hook. Syrinx is absent. Pygostyle, uncinat process and pteryiae absent

The various ratites are placed in eight distinct orders. Here only a few interesting types are described.

Struthio (family Struthionidae). Ostrich. The largest living bird with naked head and long neck, legs powerful, pes with only two digits, viz. nos 3 and 4; feathers without aftershaft. Inhabit the plains and deserts of Africa and Arabia.

Apteryx (family Apterygidae). Kiwi. Small terrestrial bird with four-toed feet; neck short; beak long and weak having the nostrils near the extremity; feathers without aftershaft and are long, hair-like and hang down loosely; wings vestigial hidden and non-functional eyes remarkably small; legs short, powerful and scaly. They are nocturnal and insectivorous or worm-eating. New Zealand.

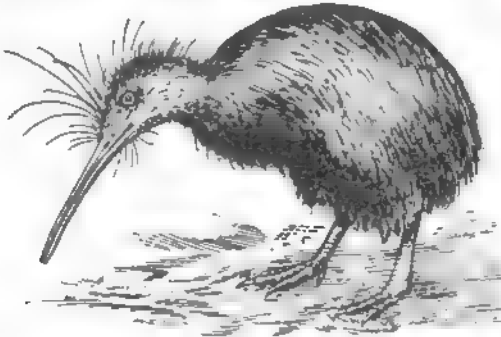


Fig. 7.79. The New Zealand Kiwi.

Rhea (family Rheidae). With partially feathered head and neck, with three toed feet, less reduced wings; and with ischiadic symphysis. Feathers without aftershaft. South America.

Casuarus (family Casuaridae). The Cassowary. With high, compressed beak, helmet-shaped bony knots on the head; with short neck, and three-toed feet. Aftershaft as large as main shaft. Australian region. *Dromiceius* or emu also occurs in Australia.

Families *Dinornithidae* (Moas) and *Aepyornithidae* are extinct.

Superorder 3. Impennae. Penguins. Eocene to Recent, The penguins (*Spheniscus*) are birds that lost the power of flight early and became especially suited to aquatic life. They swim by means of fore-limb modified into flippers. The feet are webbed. Confined to Southern Hemispheres. They come ashore to breed. Many make no nests. Throughout the incubation period the eggs (one or two) are sometimes carried on the feet.

Superorder 4. Neognathae (Carinatae). Modern birds. Includes great majority of birds, in which palatines and pterygoids articulate with the basisphenoidal rostrum; quadrate triradiate, basipterygoid processes present or absent, sternum with keel, coracoid and scapula nearly at right angle; barbules carry hooks.

Classification of the vast majority of birds involves recognition of over forty distinct orders of which the Passeriformes alone carries about half of all known species. Only a few interesting orders are mentioned below with known examples.

Order 1. Gaviiformes. Loons. These are aquatic birds or divers retaining some primitive features. *Gavia* lives on sea but breeds by lakes throughout holarctic region.

Order 2. Colymbiformes. Grebes. Aquatic, resemble divers. Lay small number of white eggs in a floating nest on lakes. *Colymbus*. (= *Podiceps*).

Order 3. Procellariiformes. Petrels. Oceanic birds leading pelagic life. *Fulmarus* (Petrels), *Puffinus* (Shearwaters), *Diomedea* (albatrosses) are examples. They lay one white egg, often in burrows.

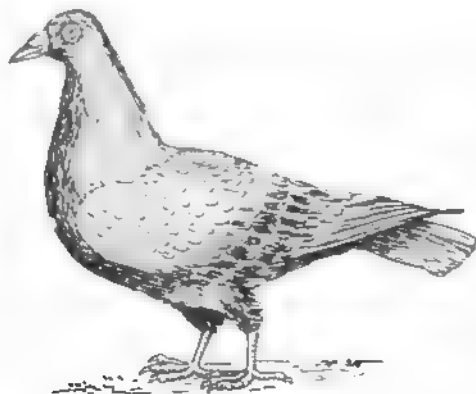


Fig. 7.20. Pigeon.

Order 4. Pelecaniformes. Cormorants, Pelicans and Gannets. They nest in colonies on rocks. *Phalacrocorax*, *Pelecanus* and *Sula*.

Order 5. Ciconiiformes. Storks and Herons. Large long-legged birds living mainly in marshes and feeding mainly on fish. Strong fliers and some are migratory. *Ciconia* (stork), *Ardea* (herons), *Phoenicopterus* (flamingos).

Order 6. Anseriformes. Ducks. Aquatic birds with flattened bill used for filter feeding in some. *Anas* (duck), *Cygnus* (swans).

Order 7. Falconiformes. Hawks. Birds of prey that hunt by day having sharp, strong curved bills and powerful feet and claws. *Falco*, *Aquila* (eagle), *Neophron* (vulture) and *Buteo* (buzzard). Eggs usually spotted. Nests made on tree-tops or on ground.

Order 8. Galliformes. Game-birds. Mainly terrestrial, grain-eating birds capable of short, rapid flight. Some structural features and habits primitive. Nests made on ground and eggs are numerous, white or spotted. Many successful types of world-wide distribution belong here. *Gallus* (Indian jungle fowl), *Phasianus* (pheasants), *Predix* (partridge), *Lagopus* (grouse), *Meleagris* (turkey), *Pavo* (peacock), *Numida* (Guinea fowl).

Order 9. Gruiformes. Rails and cranes. Mostly secretive terrestrial birds, compressed laterally, living in marshy country and having an omnivorous diet. *Fulica* (coots), *Gallinula* (moorhens), *Crex* (corncrake), *Crus* (crane).

Order 10. Charadriiformes. Waders and Gulls. Large order including the wading birds, gulls, terns and auks. Mainly live on ground often inhabiting open watery places or marshes. Often have long legs and bills, *Numenius* (curlews), *Capella* (snipe), *Calidris* (sandpipers), *Vanellus* (lapwings) and related plovers, (these are found relatively on drier lands), *Larus* (gulls), *Platystrophia* (auks, marine).

Order 11. Columbiformes. Pigeons. Tree-living, grain or fruit-eating birds mostly good fliers. *Columba*, **Raphus* (dodo).

Order 12. Cuculiformes. Cuckoos. Many cuckoos lay their eggs in the nests of the other birds, only some species build their own nest. *Cuculus*.

Order 13. Psittaciformes. Parrots. Inhabit warm climates among trees. They have considerable memory. Vegetarian.

Order 14. Strigiformes. Owls. Specialised night hunters resemble the hawks in some respects (beaks, claws, etc.). *Tyto* (the farm owls), *Asio*, (cared owls)

Order 15. Micropodiformes. Swift and humming birds. More fully adapted to air, with very long wings. Insectivorous. *Apus* (swifts); *Trochus* (humming birds).

Order 16. Coraciiformes. Bee eaters and kingfishers. Large group including *Merops* (bee-eaters) and *Alcedo* (kingfishers). Mainly tropical and often brightly coloured. The kingfishers are modified for diving.

Order 17. Piciformes. Woodpeckers. Highly specialized wood boring birds. The bill is hard and powerful. Tongue is long and protrusible. Insectivorous. *Picus* (woodpeckers).

Order 18. Passeriformes. Perching birds. This is the greatest order including about half of all the known species of birds. Small birds living quite close to the ground and have varied habits. Four toes so arranged as to allow the gripping of the perch. Many species build elaborate nests. Song is common method of display by males. *Corvus* (jackdaws), *Sturnus* (Starlings); *Fringilla* (finches); *Passer* (house-sparrows), *Alauda* (larks), *Anthus* (pipits), *Motacilla* (wagtails); *Parus* (tits); *Sylvia* (warblers); *Turdus* (black birds); *Erithacus* (robins); *Prunella* (hedge-sparrow); *Hirundo* (swallows); *Troglodytes* (wrens), etc. are only some examples of this order.

8. Class Mammalia

The mammals are the "highest" group in the animal kingdom. The name "mammal" refers to the female's mammary glands, which provide milk for her young. This characteristic alone sets off mammals among the warm blooded, back boned animals. The mammals are hairy. Most species have varied teeth for cutting, tearing or grinding. The mammal's skull is unique, the brain is more complex than in other animals. In this group the young are born alive, the parental care is mostly highly developed and reaches its climax in human species. This group includes the moles, bats, rats, rabbits, cats, dogs, horses, cows, goats, deer, whales, monkeys, man and other living forms, besides a host of extinct species and orders.

The mammals live in all sorts of habitats on every continent. They live in mountains, deserts, Arctic snows, marshes, meadows, forests, farms, cities, and the depths of the sea. Some have become adapted to specific environments, thus tree-squirrels live only in forests, rice-rats only in swamps. More adaptable mammals fit into a variety of environment, for instance, some rabbits live in woods, some in swamps, some in deserts. The mammals have developed effective ways of living. One of the most characteristic adaptive features is the care of the young inside the mother before birth. Feet with hoofs or padded toes are adapted for running, claws for digging, grasping and climbing and webs for swimming. The mammals can fly, glide, run, jump, swim, burrow and dive. Internal organs also show great adaptations. Some mammals can hibernate. It is because of such adaptations that the mammals are dominant animals today.

In size the mammals vary from the pygmy shrew and mice less than 2 inches in head and body length and weighing only a fraction of an ounce to the blue whale (*Balaenoptera musculus*) which grows to 105 feet long and 112 tons in weight. Other large species, as some carnivores and hoofed mammals, are most familiar. There are about 12,000 kinds of mammals all over the world. Some of these are rare, others so common that scores may occur on a single acre.

Many mammals are of retiring habits or nocturnal so that they are seldom seen, but they play a leading role in the present-day world. Man, the most adaptable of mammals, has domesticated and developed other mammals, as he needed. Dogs, cats, horses, cattle, sheep, and a score more have been domesticated. Most of these have been improved for human ends. The domesticated mammals provide man with food, clothing and transportation.

EMERGENCE OF MAMMALS

There can now be but little doubt that the mammals are an offshoot of the reptilian subclass Synapsida, and more particularly of some type or types of Triassic Therapsida, the true mammal-like reptiles. The latter are probably derived from primitive pelycosaur; and these in turn from the stem reptiles, Cotylosaurs. The Cynodonts, small to medium-sized active, flesh-eating reptiles are believed to be the ancestors of mammals.

These reptiles with mammal like skulls, bones and teeth lived millions of years before the dinosaurs. The first true mammals developed about 190 million years ago, but did not gain much of a foothold in the world of life until the beginning of the Cenozoic, but they began their career long before the Mesozoic, the Age of Reptiles.

and were well under way before the dinosaurs and other specialized Mesozoic reptiles had made their appearance. But the world was not ready for mammals until the great reptilian dynasties had passed. Nevertheless there are many evidences that the mammals were present and were living obscurely throughout nearly the whole Mesozoic Age. They were slowly improving themselves during this vast period, awaiting their chance to take over world supremacy. The Mesozoic was, so to speak, a period of training for the mammals. When the dinosaurs died about 70 million years ago mammals came into their own.

This therapsid reptiles approached the mammalian condition more closely than any others. These reptiles lived for the most part in South Africa in Triassic times. Abundant fossil remains of many types of these mammalian precursors have been unearthed from Karoo rocks of South Africa, and a few have been found in North America, which represent a parallel line of evolution. Of course, nothing is known about their soft parts or of their physiological peculiarities, for only their skeletons have been preserved. It has been suggested, however, that they may have been warm-blooded and may have given birth to living young, but this is pure speculation. All that is known about them must be derived from a study of their bones and teeth. The shape of the brain, of course, is known from the study of the cavity of the skulls. The bones and teeth, moreover, reveal the fact that these animals were taking on many mammalian characteristics.

It might be justified to say that if some of these therapsids continued a few steps further in the directions they had already taken, they would become mammals, but it is better to refrain from such a statement, for these particular reptiles were already rather specialized types and in some respects had gone off at a tangent from the main mammalian stock. Some of the imperfectly known later Triassic forms are closer to the main line of mammalian descent. A north American Triassic fossil jaw was formerly regarded as that of a mammal, but now has been classed as that of a theriodont reptile close to the mammalian condition. As yet it has not been possible to find any particular type of mammal-like reptile that completely qualifies as the direct ancestor of the mammals. This, however, does not cast doubt on the theory that mammals were derived from some type or types of mammal-like reptiles.

The mammal-like reptiles which were abundant during Permian and early Triassic times gradually disappeared and were apparently gone by the end of the Triassic. True mammals doubtless arose some time during early or middle Triassic times, but there are very few fossils of them from that period. Only fragmentary remains of these early primitive mammals have been found in rocks laid down near the end of the Triassic. These have been assigned to the mammalian order Multituberculata, a group characterized by extremely large and complicated molar teeth, with many tubercles.

During the succeeding period, the Jurassic, mammal fossils are more abundant and three new orders appear. Triconodonta, Symmetrodonta, and Pantotheria.

Near the close of the Cretaceous the first known Marsupials and Placentals appeared. Marsupials were at first more numerous and placentals relatively rare. All these later Cretaceous forms were small insectivorous types, as judged by the teeth. Available evidences suggest that marsupials and placentals came off independently from different types of pantotheres, the marsupials probably arising somewhat earlier than the placental mammals.

During the Palaeocene, the first period of the Cenozoic Age, the placental mammals found the world wide open for exploitation. The earliest and most primitive placentals of this period were small forms with rather generalized food habit but primarily insectivorous. Rather well-preserved skulls of rat-sized placentals of a most primitive sort have recently been found in Cretaceous rocks of Mongolia. These are not so very different in their dentition and other features from shrews of the order Insectivora. From these stem placentals split off a considerable number of independent evolutionary lines, most of which grew to larger size. During the Eocene, the second period of the Cenozoic, all the main orders of mammals had been established, apparently as offshoots of the ancestral insectivores. Several orders of these archaic placentals, notably Condylarthra, Amblypoda, Tillodontia, and Taeniodontia, became extinct before or shortly after the end of the Eocene.

TYPE RABBIT

The type for study of the Mammalia is the rabbit. In the United States and Canada the name rabbit is given to any hare. Properly, however, it should be restricted to the European *Lepus cuniculus* which differs from its relatives in being a burrower and in leaving its young born blind, naked and helpless. This is the original of the domestic rabbit whose home is believed to have been the countries which border upon the western shores of the Mediterranean. Rabbits are widespread adaptable, and able to survive in everything from hedgerows to suburban yards. Rabbits are the short-legged running species, while hares are long legged, high-jumping with young born well furred and with eyes open. The common Indian hare is *Lepus ruficaudatus*.

The rabbit is about 16 inches in length and weighs 2-4 pounds. The colour is naturally reddish brown, the under surface and the lower part of the tail being white, but domesticated rabbits show wide colour variations. Not only the flesh but the fur has a market value, chiefly as material for making felts.

The rabbits dig out extensive burrows in soft soil with the help of their fore-limbs specialized for the work. The burrow is spacious enough enabling the rearing of the family inside. The length of life of a rabbit is seven to eight years, and it breeds four times a year. Each litter may contain five to eight young which become sexually mature in four to six months. The rabbits are defenceless animals and a large number of them are destroyed by their enemies. Their gregarious habit, to some extent, is defensive. When many are feeding one can be spared to give a warning of approaching danger.

Rabbits are entirely terrestrial, gregarious animals living in burrows in sandy soil, in which they take hasty refuge when alarmed. Rabbits are mainly but not exclusively nocturnal, their favourite feeding time being early morning and evening. The diet is exclusively herbivorous, and they sometimes do great damage in plantation by nibbling the bark of trees and are excessively destructive when they obtain access to gardens.

In Australia and New Zealand the European rabbits have become a pest both to agriculture and to ranching. A few introduced from England about 1850, multiplying so enormously in the absence of enemies or destructive weather that at one time several districts seemed likely to be ruined by them. Various expedients have been tried to reduce their numbers but so far with very moderate success.

Natural enemies are birds of prey, large snakes, weasels, polecats, badgers, etc. Rabbits have been domesticated for a prolonged period and a large number of varieties are known.

Form of Body. The rabbit shows the typical mammalian form of the body—the head, the neck, the trunk (which is again subdivided into thorax and abdomen) and tail (Fig. 8.1).

At the anterior end of the body is the head containing the mouth and the anterior portion of the nerve-axis, the brain. The nostrils are immediately above the mouth and the eyes at the sides of the head. The upper lip is cleft in front (hare-lip) exposing the front teeth. From the side of the upper lip project the sensitive tactile vibrissae or whiskers. The tympanic membrane is no longer superficial as in the frog because in the mammal an outer ear consisting of a movable pinna and an external auditory meatus, has been developed. The head is freely held on the neck which gives freedom of movement to the head and enables the animal to look this way and that, to turn its ear about to determine the direction of the sound, and to perform easily endless motions in connection with biting and so forth. In the types that swim through the water (the fish and frog for instance) there is no neck, the head widening out as it passes back to the body. The high resistance offered by water necessitates this tendency to a cigar or streamline shape of the body. The neck is an extension of the body between the head and the trunk. Its development has involved alterations in the internal structures such as blood vessels and the nerves.

If the remainder of the trunk of the rabbit is examined from the outside by feeling two distinct regions can be distinguished (as one might in that of man), anteriorly a bony cage having ribs at the sides and the sternum ventrally. This portion is the chest

distal end of the postaxial¹ bone. This position of the fore arm is known as the **prone** position, and is imitated in the human arm when the arm hangs by the side with the back of the hand directed forward. Crossing of the two bones can be felt in this position. If now the arm is raised sidewise, shoulder high with the palm facing forward the two bones return to the primitive parallel position, the **supine position**. Unlike man in most other mammals the fore arm is fixed in prone position.

The position of the parts of the foot in walking is different in different mammals. The rabbit walks on the digits with the remainder of the hand and foot elevated. This mode of walking is called **digitigrade**. Man walks on the whole sole of the foot, the primitive method, known as **plantigrade**. Horses and cattle and other ungulates walk on their nails, which become broadened into hoofs. This gait of walking is called **unguligrade**.

Practically the whole surface of the body is covered by hair. The covering is distinctive of the class of animals called mammals, in birds there is an equally characteristic cover in feathers, the frog is naked, fishes have either naked or scaly skins.

THE SKIN

The bodies of all vertebrates are invested by an outer covering called the **integument** or **skin**. The integument has several important functions: the formation of a pliable covering for the body, resistant to the entrance of foreign materials, the regulation of body temperature, the prevention of wastes through the sweat glands, the development of sense organs and the formation of special coverings and appendages.

The skin of mammals is thicker, both the epidermis and dermis contributing to its thickness. The characteristic of the mammalian skin is the presence of hair, which form an insulating layer by entangling air between them in order to maintain the body temperature. Sweat or sudorific glands of the skin also help in maintaining the temperature. Epidermal glands are diverse. Epidermal scales are present in restricted areas and dermal scales are present only in armadillos. Normally during rest the hairs lie parallel to the skin surface, but they are movable and have definite muscles for the purpose. Hairs are not comparable morphologically with either feathers or scales

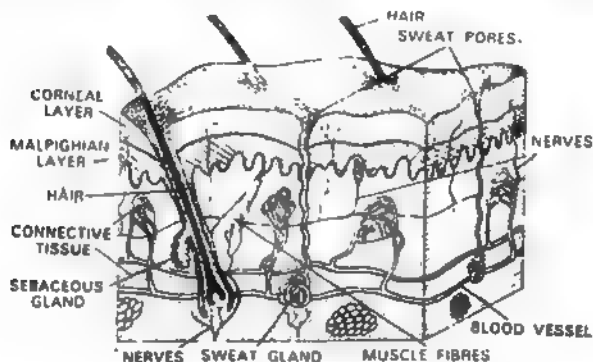


Fig. 8.2. Diagram showing the structure of mammalian skin.

If the right arm is extended horizontally outwards from the shoulder, with the palm and hand vertical and the thumb upwards it will show the following surfaces and borders, a ventral or flexor surface, a dorsal or extensor surface, a preaxial border along which are the thumb and the radius and a post-axial border along which are the little finger and ulna.

since their development is initiated by epidermis and not dermis. Phylogenetically the scales are older than hairs as is evident by the fact that scales appear earlier in the embryo.

Structure of Hair. Each hair consists of a root (Fig. 8.3) buried in the skin and a shaft projecting from it. The root is lodged in a pit-like invagination of the epidermis called a hair-follicle. It is swollen at the base forming a bulb, below which lies a concentration of vascular dermal tissue, the dermal papilla, which feeds the hair. The root is surrounded by epithelial and connective tissue sheaths the root sheaths, which can be distinguished into an external root sheath and an internal root sheath¹. The shaft of the hairs is made up of three layers, an outer cornified layer, the cuticle, the next layer is called cortex and the central layer is medulla. The cuticle is made up of scale-like overlapping cells. The cells of the cortex are elongated and form the greater part of the hair. The medulla is made up of cuboidal cells arranged in a double row. The medulla is wanting in finer hairs and occurs only in the stouter ones which are referred to as contour hairs by some authors.

Development of Hair. The cells of the germinative layer of the epidermis start multiplying at any one place, where a hair has to appear, forming a concentration of epidermal cells. This concentration increases in size due to rapid growth and sinks into the corium (Fig. 8.3 B) and forms the hair germ. The tip of the air germ enlarges forming a bulb at the base of which some dermal cells accumulate (Fig. 8.3 C, D). These dermal cells form the dermal papilla that provides nourishment to the developing hair. Now the cells of the germinative layer just in contact with the dermal papilla produce by rapid multiplication a conical shaft of the hair. The cone grows for some time and then separates from the surrounding cells as they split off. The basal portion of the shaft, thus separated, is the root of the hair. As the development proceeds the cells of the root become horny. The lining of the follicle is also somewhat cornified and is known as the outer root sheath. This clings to the hair as a white coat when the hair is pulled out. The sheath later on differentiates further forming a thin inner root sheath. The shaft grows more and more and finally emerges out after piercing through the epidermis. The hairs emerge at an acute angle having a slant in some special directions. This is responsible for the formation of streams (of hairs) on various parts of the body. Where such currents meet either rhomboids or vortices are produced. The vortices are usually called cowlicks. Such rhomboids and vortices also appear on human body and are evident in regions where hair is short.

Hair Arrangement. The arrangement of hair suggests that they may originally have been interscalar (originating between scales) in position. The hair occur in isolated groups of two (Fig. 8.4) to a dozen or more depending upon species. These groups are arranged in parallel rows in such a way that each group lies opposite an interval in the rows in front and behind. In short the arrangement is imbricated, like the universal arrangement of the scales. The distribution of hairs, therefore, seems to indicate that at one time mammals may have been covered with both scales and hairs (as in the scaly anteaters and armadillos).

Other Epidermal Structures. The hair are variously modified to form various structures such as the horns of rhinoceros, scales of the scaly anteater, spines in spiny anteaters, quills of porcupines or bristles, etc.

In the amniotes as a whole the stratum corneum gives rise to epidermal scales, claws, nails, horns, spikes, beak-covering (turtles, bird, duck-bill), spur coverings, feathers and hairs. The epidermal scales are characteristic of reptiles and in birds and mammals they may be present in restricted areas. The claws are characteristic of most of the reptiles, birds and mammals. In the mammals the claws may be modified as nails and hoofs. The horns, characteristic of ungulate mammals are also found in some reptiles. The horns of mammals are of four types. (i) the hair-horns, (ii) the antlers, (iii) the true-horns and (iv) giraffe-horns. The hair-horns are modified from hair and occur in *Rhinoceros*. They are composed of agglutinated modified hairs. The antlers are branched bony horns characteristic of deer-family and are shed annually. During the

¹The inner root sheath is two cells thick, of which the outer is Henle's layer and inner Huxley's layer

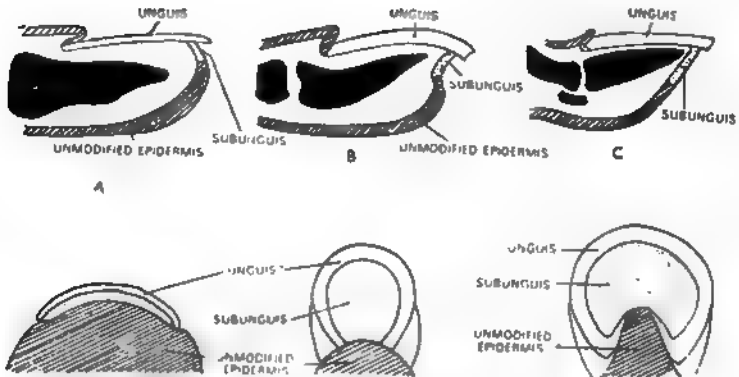


Fig. 8.5. Diagram of nails (A), claws (B) and hoofs (C) (based on Boas from Kingsley).

development stages the antlers are covered with soft skin or "velvet" which soon wear off leaving naked bone. Antlers occur in males except in reindeer. Antlers are not integumentary structures. True-horns are present in the bovine animals such as the cattle, sheep, and antelopes. They have a bony core covered with a horny epidermal cap that is not shed except in the case of pronghorn antelope, in which the horny covering is shed annually. The true horns are never branched, never shed and usually occur in both sexes. In the true horns once again there is a modification of the stratum corneum forming the epidermal cap. The *giraffe-horns* (Fig. 8.6) are stunted antlers covered always with unmodified epidermis.

The glands of the integument are all epidermal and of different types. In fishes large number of skin glands are present, but they are unicellular. In the tetrapods the skin-glands are multicellular and abound in amphibians but are rare in reptile and birds. In mammals the skin-glands are numerous and diversified. These include the mammary glands, the sudoriferous glands, the sebaceous glands and scent glands, etc.

The mammary glands are milk-secreting epidermal glands or *mamma* characteristic of the mammals. They are believed to be modified tubular glands, possibly derived from sweat glands. In monotremes the simplest type of mammary glands occur. Here the glands are branched-tubular and produce a nutritious secretion instead of milk. In place of regular nipples tufts of hair are present. The young monotreme does not have muscular lip and is further handicapped by a horny beak. It is, therefore, unable to suckle. It licks the nutritious sweat from the tufts of hair with its protusible tongue. In *Echidna* a temporary pouch or *incubatorium* surrounds the mammary area, which is lacking in *Ornithorhynchus* in which case the ventral mammary area is depressed and tufts of hair, serving as nipples, project from the depression. In marsupials there is a slight nipple developed from the bottom of the pocket, which in the opossum are hygienically lodged in a depression within the skin when not in use.

In higher mammals first a ridge, the *milk line*, appears on either side of the body from in front back to the inguinal region. Soon this breaks up into *milk points*, the intermediate part of the milk-line, between the milk-points, disappears. Each of the points may develop into a definite *milk gland* or *mamma*, but all of them do not develop fully. For this reason the number in the adult is less than that in the embryo.

The number and distribution of mammae (hence of nipple or teats) differs with species. In apes and man single pair of thoracic teats occur. The tree dwellers among these are required to carry the young in the arms. Similar thoracic teats occur in bats also. Flying lemurs have a single pair of *axillary* teats situated in the arm-pit, while in the Cetacea teats occur in the groin and are grown as *inguinal teats*. In this case the baby porpoise or whale holds on to the teats like ectoparasite (baby trailer) as the mother swims in water. Insectivores have two pairs of teats, one thoracic and one

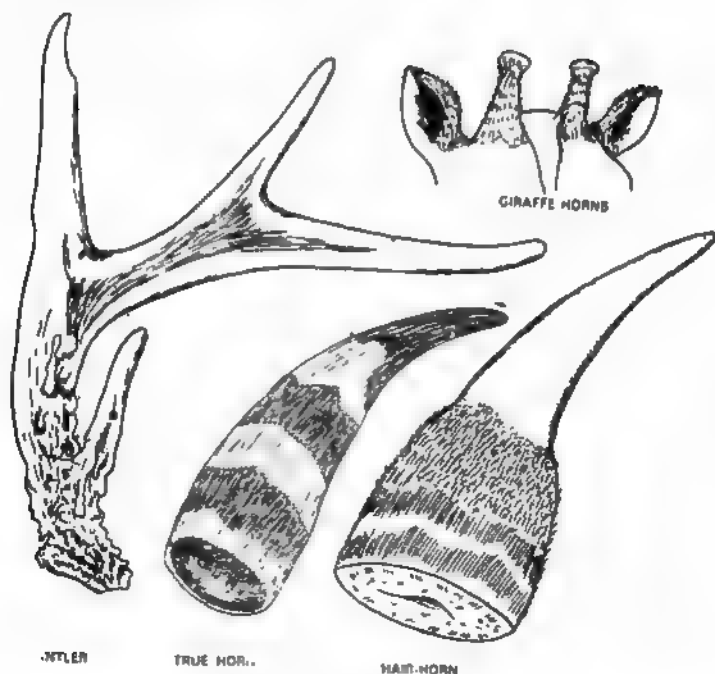


Fig. 8.6. Different types of horns.

inguinal. Many mammals such as pigs, dogs, edentates, etc., have a series of teats scattered all along milk-line including **axillary thoracic**, **abdominal** and **inguinal**. Generally speaking there is a provision for the number of young in a litter. Besides these additional or **supernumerary teats** may develop in any mammals including man. It is interesting to note that the mammary apparatus develops equally in both the sexes up to the time of puberty, when it degenerates in the male and becomes potentially functional in the female.

The teats or nipples may be of two types, **true** and **false** nipples. In true nipple the gland-bearing area becomes elevated and the ducts open at the tip of the nipple. In the false-nipple the ducts open in a depression and the skin around this depression becomes elevated forming what is called a **milk-canal**. The glands empty at the bottom of the milk-canal which conducts it to the outside.

Other Modifications. The tips of the human fingers reveal fine **friction ridges**, that prevent the fingers from slipping when brought into contact with objects. The arrangement of ridges shows different patterns, but in most they are arranged at right angles to the direction in which there is the greatest tendency to slip. Sweat glands, opening on the ridges help to make the grip firm. They are mostly developed in the **palmar** and **plantar** surface of the hands and feet of man and other primates, the surfaces (Fig. 8.8) that come habitually into contact with other objects.

Friction areas are associated with pad-like epidermal cushions or **tori** that appear on palm and soles. Typically ten tori occur on each hand or foot, five **digital** at the tips of fingers or toes, three **interdigital** near the base of the digit, one **thenar** at the

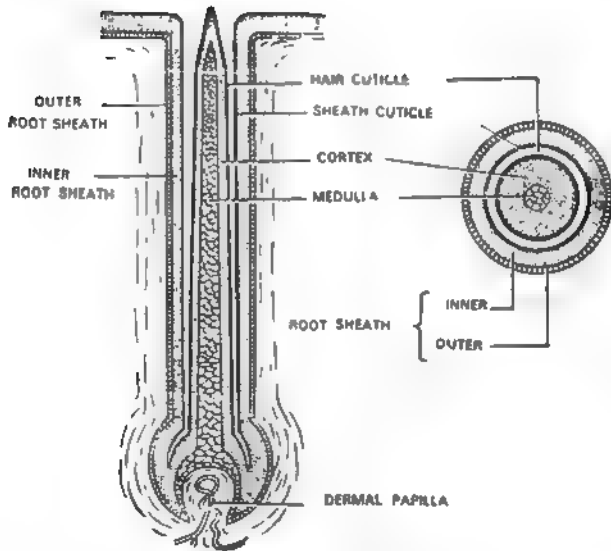


Fig. 8.10. Longitudinal and cross-section of the hair along with the hair follicle of mammal.

outpushings of follicular wall, and these secrete an oily substance on to the hairs which keeps them supple and prevents them from becoming wetted with water. This is a very necessary precaution especially in mammals which live or hunt in water. Although the above description covers any typical portion of the skin in certain regions modifications may occur. In the region around the mouth the hairs may become very long and strong forming the *vibrissae*. In regions where the skin is subjected to considerable friction, such as in the under surface of the feet, the stratum corneum becomes extremely thickened forming the *familiar pads* and in human beings, *callosities*. At the tip of the digits strong *claws* or *nails* may be present and in some mammals the digits terminate in *hooves*. In these cases specially hard material known as *keratin* is produced.

Another cutaneous development is the *mammary gland*. These are modified *sebaceous glands* (except in some lower mammals) which have been highly concentrated and enlarged. They secrete the fluid milk upon which the young mammal lives for some time after it has entered the world.

Muscles. Immediately beneath the skin the whole ventral region of the trunk and neck is covered by a thin *cutaneous muscle*, that enables the rabbit to twitch its skin. The mammary glands of the female lie internally to this muscle. Along the mid-ventral line of the abdomen passes a whitish band of connective tissue extending from the xiphisternum to the pubis. This separates the musculature into two longitudinal bands, the *recti abdominis*. Laterally to them the abdominal wall consists of three thin layers of muscles with their fibres running in different directions. These are the *external oblique*, the *internal oblique* and the *transversalis*, the latter being lined on its inner surface by the peritoneum. A fibrous cord (*Poupart's ligament*) extends upwards and forwards from each pubis to the corresponding ilium. Beneath this ligament pass the blood-vessels and nerves outwards to the leg. The muscles of the body wall in the thorax are broken up into a series of *intercostal muscles* by the ribs. Like the oblique muscles of the abdomen the intercostal muscles are also arranged in two layers, *external* and *internal*, and aid respiration. Extending from the thorax to the fore-limb

Fig. 8.10. *Homomys* of the rabbit.

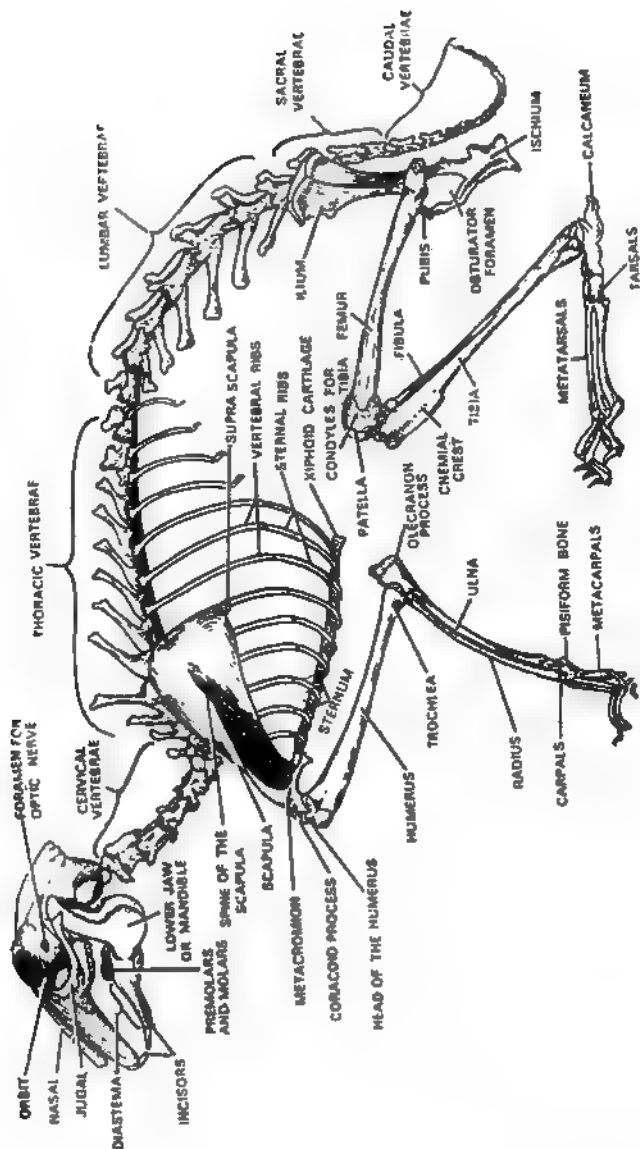


Fig. 8.11. Articulated skeleton of a rabbit.

bulia. A large median supra-occipital completes the occipital ring above its outer surface is raised into a prominent shield-shaped elevation, giving attachment to the muscles raising the head.

The **parietal ring** (posterior sphenoid region) consists of both cartilage bones and membrane bones. Its base is formed by the **basi-sphenoid** which lies in front of the basioccipital. It is a triangular bone directed forwards. On its dorsal surface there is a depression, the **sella turcica**, lodging the pituitary body in life. This is bounded by the large overhanging **posterior clinoid process**, while its floor remains unossified as the pituitary foramen. The sides of this ring are formed by a pair of wing like bones, the **alisphenoid**. From the ventral surface of each alisphenoid there projects downwards a vertical plate of bone, the **external pterygoid process**, which is connected along its inner edge with the palatine bone. At the base of the alisphenoid there are three

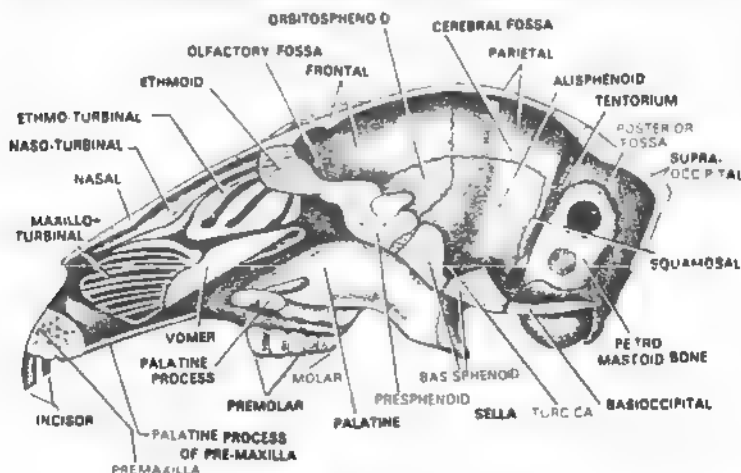


Fig. 8.19. Sagittal section of the skull of rabbit.

foramina, of which the largest innermost transmits the internal maxillary artery and vein, and the two outer ones transmit branches of the mandibular division of the fifth nerve. Between the alisphenoid and the anterior end of the basisphenoid is a large slit-like notch the **sphenoidal fissure** (**foramen lacerum anterius**) through which the third, fourth and sixth nerves and first and second divisions of the fifth nerve pass out from the cranial cavity. At the posterior border of the alisphenoid there is an opening, the **foramen ovale**, for the exit of the third division of the fifth nerve. The roof of this ring is formed by flattened membrane bones; the **parietals**, which meet in the mid-dorsal line. A small median **interparietal** (membrane bone) lies between the parietals and supraoccipital.

The **frontal ring** consists of a laterally compressed median bone, the **presphenoid**, the paired **orbitosphenoids** forming the sides and the membrane bones the **frontals** forming the roof. The presphenoid is connected to the basisphenoid by cartilage. It forms the lower margin of the **optic foramen**, a large aperture for the exit of the optic nerve. The upper and posterior border of the presphenoid is produced backwards into the small **anterior clinoid process**, binding **sella turcica** in front. The orbitosphenoids are large lamellar bones which surround the optic foramen. In front of the optic foramen the orbitosphenoids are continued forwards as a pair of vertical laminae forming parts of the inner walls of the orbit. The frontals are large membrane bones forming the roof and sides of this region. They unite suturally in the mid-dorsal line

and with the parietals behind. The outer surface of each frontal forms the upper part of the wall of the orbit and bears a prominent crescentic **supraorbital process**. A slender process of the frontal runs in front between the maxilla and premaxilla.

Cranial Cavity The interior of the cranial portion of the skull is occupied by a large cavity divisible into three regions of unequal size (Fig. 8.19). The most posterior regions enclosed within the occipital and squamosal bones is the **posterior or cerebellar fossa** of the skull. Its anterior boundary is marked by a slight (rabbit) ridge or shelf of bone, the **tentorium**, which in life is completed by a membrane. In the lateroventral wall of the cerebellar fossa is a rounded area of very hard compact bone bearing two openings, this is the **petrous** part of the **petromastoid bone** and encloses the internal ear. The greater part of the cranial cavity comprises the middle or **cerebral fossa**, extending forward from the tentorium. Its roof and walls are formed by the frontal, parietal, and squamosal bones, its floor by the sphenoids. In the floor of the cerebral fossa, located in the basisphenoid bone, is a marked saddle-shaped depression, the **sella turcica**, in which in life the pituitary body is lodged. The presphenoid bone contains a cavity, the **sphenoidal sinus**. In the anterior part of the frontal bone, cavities known as the **frontal sinuses** are also present. The anterior end of the cranial cavity is the small **anterior or olfactory fossa** located between the anterior parts of the two frontal bones. The olfactory fossa is separated from the nasal cavities which lie in front of it by a nearly vertical plate of bone, perforated by numerous holes, the **cribriform plate** of the ethmoid.

Olfactory Capsule. The **ethmoid region** lies entirely in front of the cranial cavity and is closely related to olfactory organs. It encloses nasal cavities which are separated from the cranial cavity by a nearly vertical plate of bone the **cribriform plate**, perforated by numerous holes as in a sieve. The nasal cavities are enclosed partly in cartilage bones, derived from the ethmoid plate, and partly by membrane bones. The roof of the cavities consists of the **nasal bones** and a small part of the **frontals**. The two cavities are separated by a median, vertical, bony partition, the **perpendicular plate** of the ethmoid, in the living state this is continued to the anterior nares by a cartilaginous plate. The two together constitute the **septum of the nose** (internal septum). The bony part of the septum, that is, the perpendicular plate of the ethmoid, is small in the rabbit. Dorsally the septum meets the nasal bones; ventrally it meets the **vomer**, an elongated bone dorsal to the maxillae and palatines. The posterior end of the septum meets the cribriform plate.

On the half of the skull where the septum is missing the turbinated bones or **conchae** are present. They are peculiar, delicate, grooved bones which occupy the lateral walls of the nasal cavities and fill most of the interior. The most posterior of these bones is the **ethmoturbinal** or **ethmoid labyrinth** situated just in front of the cribriform plate. It is a greatly folded structure, the folds enclosing spaces known as the **ethmoid cell**. In front of the ethmoturbinal is another but smaller mass, the **maxilloturbinal**, borne on the inner surface of the maxilla. Each nasal bears on its inner surface a single elongated ledge of bone, which constitutes the **nasoturbinal**, and which lies above the uppermost scrolls of the ethmoturbinals. The function of the turbinals is to increase the respiratory and olfactory surface of the nose. The ethmoturbinals are covered by the olfactory epithelium, while the maxilloturbinals serve to strain and moisten the air. The latter project into the passage from the anterior to the posterior nares.

From the comparative standpoint the septum of the nose is the **mesethmoid**, the perpendicular plate of the ethmoid being its ossified portion, while the ethmoid labyrinths are the **ectethmoids**. The cribriform plate is produced by the extension of ossification processes between the mesethmoid and ectethmoids. The perforations in the plate are for the passage of the olfactory nerve. Thus, the three ethmoid bones of lower vertebrates are fused into the single ethmoid bone of mammals.

Orbit. The orbit is formed by several bones like the orbitosphenoids, alisphenoids, etc. In the anterior wall of the orbit is the **lacrimal bone** (probably homologous with the prefrontal bone of reptiles) on each side. Each lacrimal is a lamellar bone wedged in between the frontals and maxilla. At the anterior end of the lacrimal bone is an opening, the posterior end of the nasolacrimal duct, by means of which the tears drain into the nasal cavity.

differentiated in relation to the presence of the chief organs of sense, the brain, the mouth and the respiratory gill-slit (cephalization). Thus, the head and trunk, that possess basically similar segments in the beginning become specialized in divergent directions. As a result of cephalization the primitive segmentation disappears in the finished product. Cephalization is more prominent in higher than in lower forms and in older than in younger stages of development.

Closer study by various stalwarts¹ emphasizes that in vertebrates, segmentation is primarily expressed in the mesoblastic tissues. It is, therefore, the mesoblast that furnishes the most convincing evidence. Recall that in the trunk of the craniate the more dorsal part of the mesoblast forms segmental somites and sclerotomes from which segmental myotomes (myomeres) and skeletal elements are derived respectively.

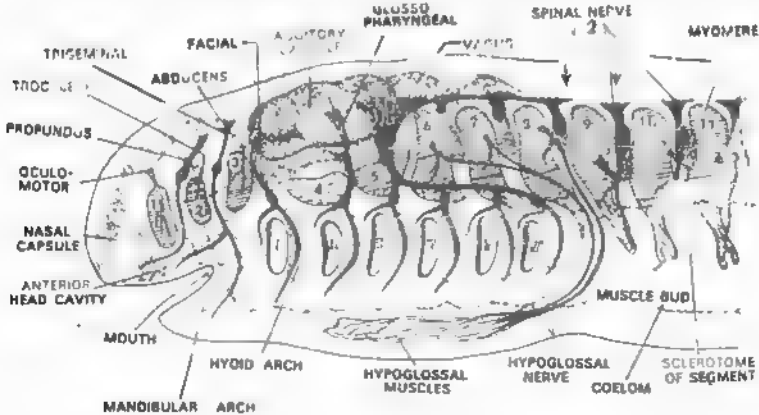


Fig. 8.23. Diagram illustrating the different segments of the skull of a dog-fish (after Goodrich).

The segmental nerves also correspond to these. A ventral motor root supplies each myotome and a dorsal root (chiefly sensory) passes behind it.

In the head also segmentation extends to a point just behind the hypophysis, where the notochord merges into the original roof of the archenteron, from the side walls of which the mesoblast develops. The mesoblasts become subdivided into dorsal segmented somites and ventral unsegmented lateral plate. The head somites are of the same nature as those of the trunk in form and structure. The muscles developing from the head somites are supplied by ventral motor nerve root of its segment. The corresponding dorsal ganglionated root passes behind each somite. The gill-slits pierce the lateral plate intersegmentally. Visceral arches are, thus, formed, and down each passes the dorsal nerve root supplying motor fibres to the visceral muscles. It follows, therefore, that the segments of the head region are similar to those of the trunk and that they have their own ventral and dorsal nerve roots which, of course, do not meet as in the case of the ventral and dorsal roots of the trunk region. The cranial nerves corresponding to the dorsal roots are all ganglionated, whereas, those of the ventral roots are not.

The primitive uniform disposition of the segment is disturbed by the development of the sense capsules in the head region. The auditory capsules separate three anterior pre-auditory or pro-otic somites from the post-auditory or meta-otic somites. The pro-otic somites give rise to the muscles of the eye, which are extraordinarily constant in number, disposition and innervation in the vertebrate series. The first segment or

¹Balfour (1874-78); Marshall (1882); Wijhe (1882); Gegenbaur (1872); Stohr (1879, 1881, 1882); Rosenberg (1884); Saguchi (1891); Frorich (1905), etc.

interior of the mandible to the mental foramen. In the rabbit there is an additional foramen just above the mandibular foramen, for the passage of a vein.

Owing to the absence of the quadrate and of all the bones of the lower jaw except the dentary the articulation of the lower jaw to the skull is between the dentary and squamosal. The squamosal is a slightly curved plate of membrane bone, which completes the side wall, of the cranial cavity lying in front of periotics, and articulating with the parietals, frontals, orbitosphenoids and alisphenoids. A slender **post-tympanic process** arches backwards, from the hinder border of each squamosal, over the external auditory meatus. From its outer surface arises a stout **zygomatic process**, which bears on its under surface the articular facet for the mandible. Beyond the facet it bends downwards to articulate by an expanded end with the jugal bone forming the zygomatic arch.

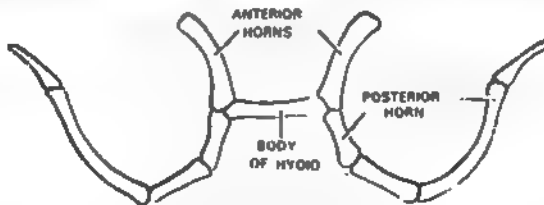


Fig. 8.24. Hyoid apparatus of the rabbit.

The **hyoid apparatus** lies in the floor of the mouth between the rami of the mandible. It consists of a median body and two pairs of backwardly projecting cornua of which the posterior are larger. The anterior cornua are the ventral of the hyoidian arches, the dorsal end of each of which has aborted. The middle piece has separated off as a small bone (**stylohyal**) attached to the paroccipital process. The posterior cornua are the lower ends, and only persistent part of the first pair of branchial arches (Fig. 8.23).

APPENDICULAR SKELETON

The **appendicular skeleton** consists of the skeleton of the two pairs of limbs and the girdles that support them. The bones of the limbs are mostly elongated and provided with epiphyses at their ends.

Pectoral girdle and Fore-limbs. The pectoral girdle of most mammals is reduced and somewhat modified. Only the monotremes have complete pectoral girdles, consisting of scapula, coracoids, clavicles, and interclavicle (Fig. 8.25 A). In all of the placental animals, the coracoid is reduced to a small process, the coracoid process, that interclavicle is missing, and the clavicles are often reduced or wanting (Fig. 8.25 B). Consequently the pectoral girdle of most mammals consists of the **scapulae** only which are correspondingly enlarged and are important as places of muscle attachment.

The pectoral girdle of the rabbit consists of two pairs of bones the clavicles and the scapulae. The clavicles are small slender bones imbedded in the muscles of the front of the shoulder, and as they are not articulated to the rest of the girdle they generally fall off in prepared skeletons. The scapula or shoulder blade is the large, flat triangular bone, situated dorsal to the anterior ribs. The mammalian scapula has certain characteristics which differentiate it readily from the scapulae of other vertebrates. It is triangular in form, the apex of the triangle articulating with the humerus. Its outer surface bears a prominent ridge, the **spine of the scapula**. The ventral end of the spine terminates ventrally in a pointed projection, the **acromion process**; just above this and projecting laterally and posteriorly is the long **metacromion process**. The apex of the scapula is concavely curved forming the **glenoid fossa**. From the anterior side of the rim of the fossa a small beak-like process projects medially; this is the **coracoid**

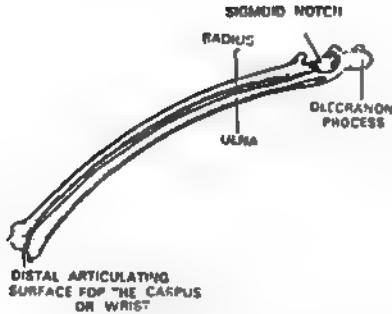


Fig. 8.27. Radius and ulna of the rabbit.

trochlear foramen. The posterior or olecranon fossa is the larger of the two and lodges the olecranon process of the ulna when the arm is extended.

The forearm consists of **radius** and **ulna**, of which the latter is the larger. The proximal end of the ulna forms a prominent projection, the **elbow** or **olecranon**. Distal to this is a deep semicircular concavity, the **semilunar notch**, which articulates with the trochlea of the humerus. The distal border of the notch forms another projection, the **coronoid process**. The proximal end of the radius is situated lateral to or in front of the proximal end of the ulna, while its distal end is medial to the distal end of the ulna. In

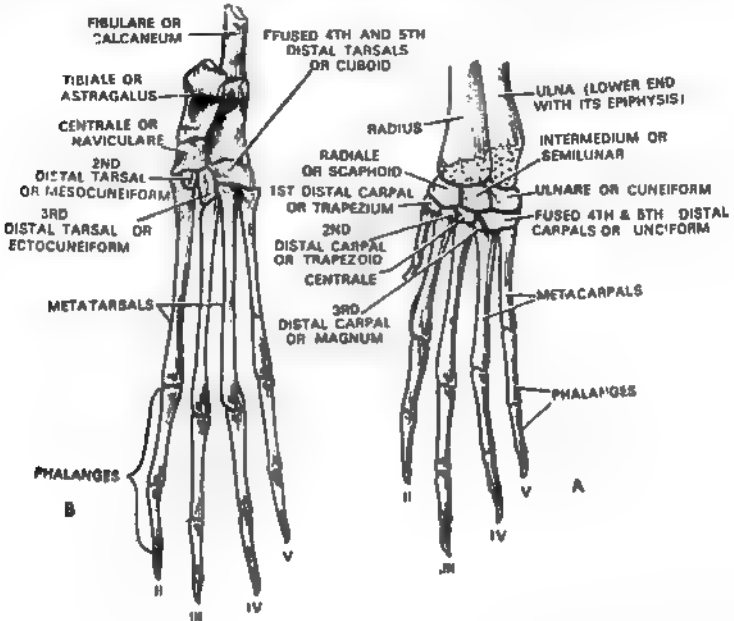


Fig. 8.28. Skeleton of Hand. Rabbit appendages. A, the wrist and metacarpals; B, bones of the ankle and foot.

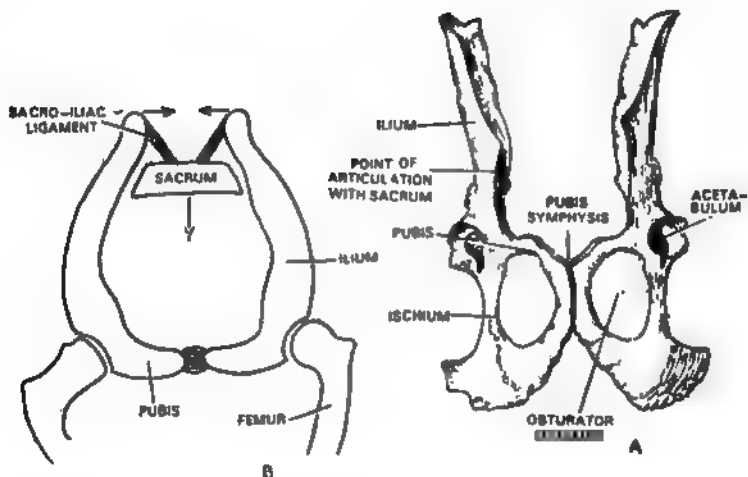


Fig. 8.30. Pelvic girdle of the rabbit (A) and (B) Relation of pelvic girdle and limbs in a mammal. The sacrum functions as a keystone although upside down because of the sacroiliac ligaments. Greater the weight from above, the more the iliacs tend up, pinch together holding the sacrum in place (After Meyer).

greater part of its length. The anterior face of the tibia presents a crest; its proximal articulating surfaces are known as condyles; its distal ones as malleoli. The bones of the ankle are identical with those of the human ankle and are designated by the same names, which are, unfortunately, somewhat fanciful and not based upon comparative anatomy. The name derived from comparative anatomy is given in parenthesis after

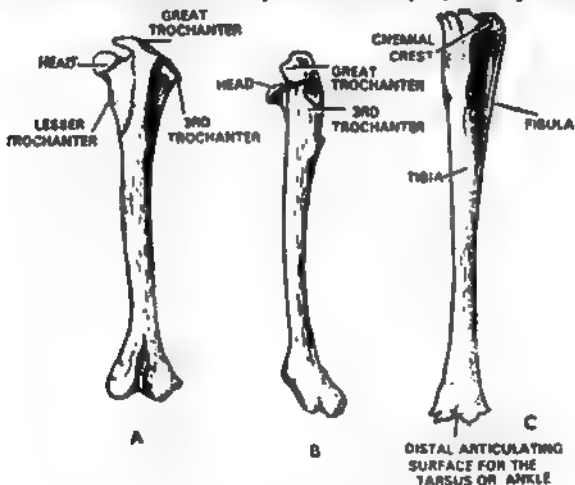


Fig. 8.31. A, B, femur of the rabbit; C, tibia and fibula of rabbit.

region. Each of these regions contains cavities which are partitions of the coelom. The **thoracic coelom** is divided into three portions, two laterally situated **pleural cavities** and the median **pericardial cavity** located between the former. The pleural cavities lodge the soft spongy lungs, whereas, the pericardial cavity accommodates the heart. A delicate partition, the **mediastinal septum**, stretches from the heart to the median ventral line. It is made up of two medial walls of the right and left pleural cavities in contact with each other. At the level of the heart these walls separate enclosing the pericardial sac between them. The space between the two walls of the mediastinal

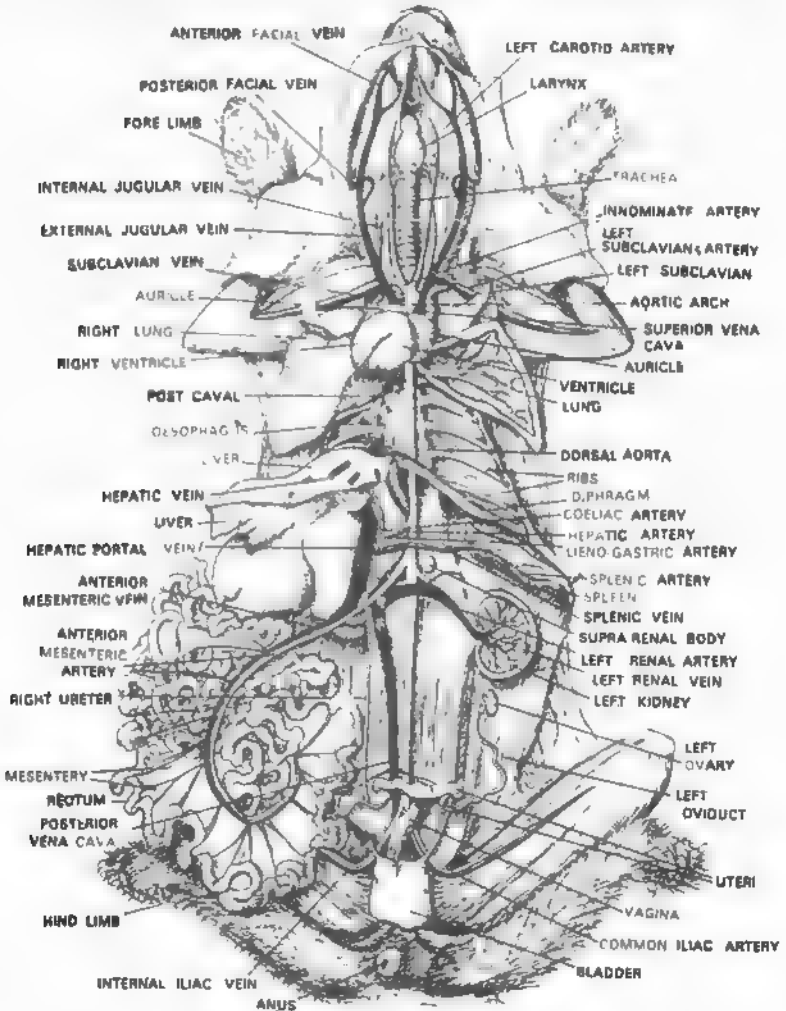


Fig. 8.33. Organs of the body cavity of the rabbit.

septum is called the **mediastinum**. The posterior wall of the pleural cavity is formed by dome-shaped muscular partition, the **diaphragm**. A moist membrane, the **pleura**, lines the pleural cavity. It is a part of the peritoneum. The pleura is divided into **parietal** and **visceral** parts. The **parietal pleura** covers the inner side of the pleural cavity, and the anterior face of the diaphragm and forms the mediastinal septum in the mid-ventral line. The **visceral pleura** covers the lungs to which it is indistinguishably fused.

The **pericardial coelom** is enclosed by thin **pericardium**, an extension of the peritoneum, which is not attached to the heart except at the anterior end where the great vessels enter and leave the heart. Inside the pericardial cavity the heart is freely movable. The surface of the heart is invested by the **visceral pericardium** that is inseparably fused to the heart wall. The **parietal pericardium** is separated from the heart by the pericardial cavity. As the heart lies in the mediastinum the parietal pleura of the mediastinal septum forms the third layer of coelomic epithelium surrounding the heart. The **thymus** is also situated in the mediastinum ventral to the anterior part of the heart.

Abdominal Coelom. The thoracic coelom is separated from the abdominal coelom by a curved muscular sheet, the **diaphragm**. The cavity posterior to the diaphragm is the large **abdominal** or **peritoneal cavity**. This cavity is lined by a membrane, the **peritoneum**. The portion of peritoneum inside the body wall is the **parietal peritoneum** and that extending over the visceral organs is the **visceral peritoneum** or **serosa**. In passing to and from the body wall to the viscera the peritoneum forms double-walled **mesenteries** or **ligaments**. The **dorsal mesentery** is intact in mammals and the **ventral mesentery** persists in the region of the liver and urinary bladder.

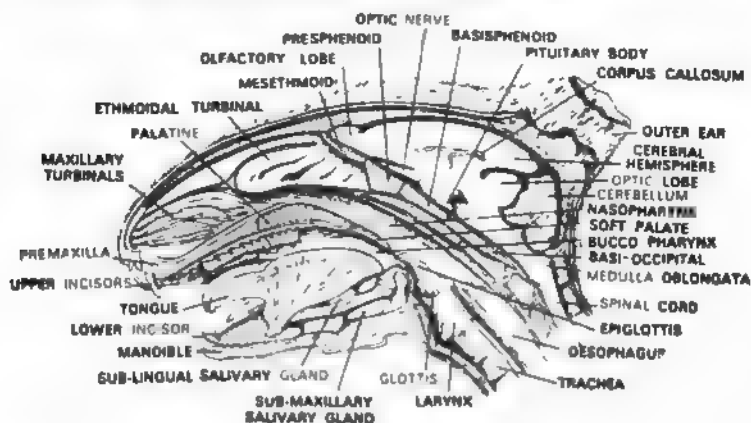


Fig. 8.34. Sagittal section of the head of the rabbit.

Viscera. As is evident from the above the lungs and the heart are the major organs occupying the thoracic coelom. The organs of the peritoneal cavity include the liver, alimentary canal, excretory and reproductive organs, etc. Fitting into the concavity of the diaphragm is the large dark-red lobed liver. Posterior to the liver the cavity is filled by the coils of intestine, which is covered by a thin membrane impregnated with streaks of fat. This is the **great omentum** more conspicuous in other mammals than rabbit. At the posterior end of the peritoneal cavity lies the pear-shaped **urinary bladder**. The **stomach** lies dorsally to the left lobe of the liver. The **spleen** is attached to its left border. At about the level of the posterior ends of the liver lobes occur the bean-shaped **kidneys** on the dorsal wall of the abdominal cavity. In the female rabbit **oviducts** and the horns of the **uterus** (prominent in pregnant females) are visible. The **testes** in the male lie in the scrotal sacs not in this part of the peritoneal cavity.

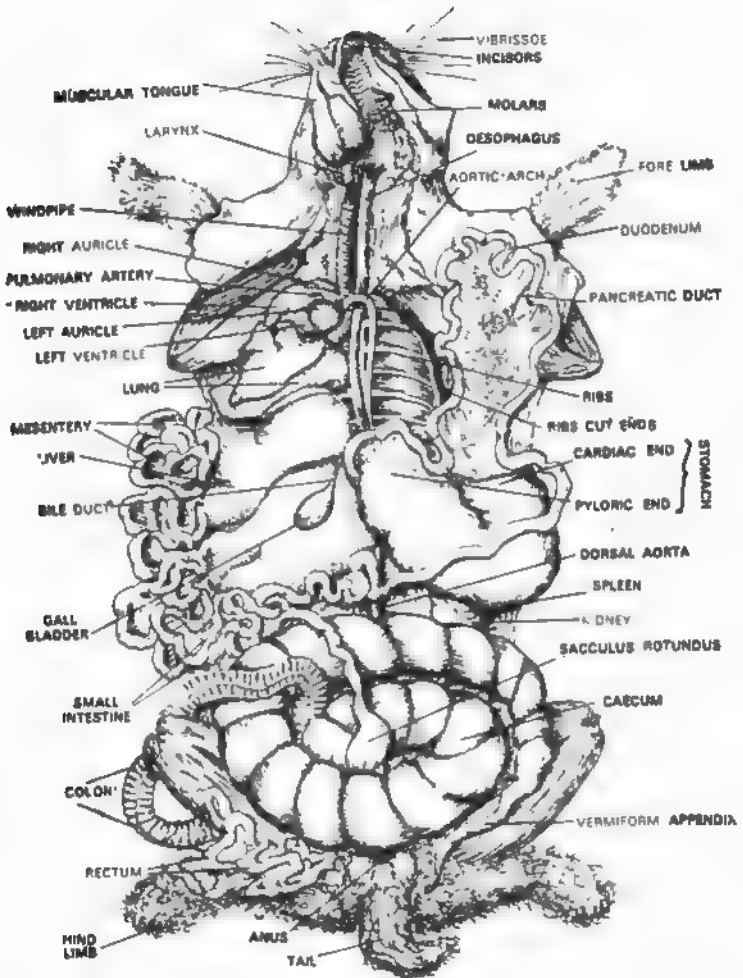


Fig. 2.35. Digestive organs of the rabbit.

DIGESTIVE SYSTEM

Oral Cavity. The mouth or oral cavity marks the beginning of the digestive system. It is enclosed by the lips and cheeks. The part of the oral cavity lying between the teeth and lips is the vestibule of the mouth. The anterior portion of the roof of the oral cavity is occupied by the **hard palate**, the posterior part by the **soft palate**, which is very long in the rabbit. The hard palate is supported by the premaxillary, maxillary and palatine bones, the soft palate is without bony support. The mucous membrane of the hard

palate is thrown into a number of roughened transverse ridges. At the anterior end of the hard palate just behind the incisor teeth occur a pair of openings, the openings of the nasopalatine ducts which connect the mouth and nasal cavities by way of the incisive foramina of the maxillary bone.

The floor of the oral cavity is occupied by the tongue, a fleshy muscular organ, more mobile in mammals than in most other vertebrates. The anterior margin of the attachment of the tongue to the floor of the mouth has the form of a vertical fold, the frenulum. Halfway between the lower incisors and the frenulum are located in the rabbit the two small slit-like openings of the ducts of the submaxillary glands, the two being about one-eighth of an inch apart.

In the rabbit the tongue is divisible into two portions, an anterior softer portion, covered with minute pointed elevations, the fungiform papillae, and a posterior elevated, smoother, and harder portion. At the posterior end of the latter, on each side, is situated a vallate papilla, consisting of a round elevation set into a pit. In front of each vallate papilla on the side of the tongue is an oval area of considerable size marked by numerous fine parallel ridges, the foliate papilla. The papillae are provided with microscopic taste buds.

Salivary Glands. The salivary glands are masses of glandular tissue that pour salivary secretions in the mouth cavity. They are outgrowths of the lining of the mouth cavity, the stalk of the outgrowth persisting as the salivary ducts. These glands are situated in the head and throat. In the rabbit there are four pairs of salivary glands.

The Parotid gland is the largest of all the salivary glands and is located below and in front of the base of the pinna of the ear just under the skin. They are pinkish glands spread out under the skin anterior and ventral to the ear. It may extend up to the angle of the jaw and some distance forwards along the inner surface. The duct of the parotid (stemonian duct) leaves the gland at its anterior border and runs forwards just beneath the skin and opens on the inner side of the cheek opposite the second upper premolar tooth. The submaxillary gland is a compact roundish mass of reddish colour lying close to its fellow between the angles of the mandible, and in front of the larynx. Its duct is called Wharton's duct that leaves the outer side of the gland and runs forwards along the inner side of the jaw opening into the floor of the mouth midway between the lower incisors and the root of the tongue. In the path of the submaxillary duct is located a small elongated flattened reddish body, the sublingual gland, which opens on the floor of the mouth by several short ducts. The infraorbital gland is an irregular lobulated mass about three-quarters of an inch long, lying below and in front of the eye. Its duct runs downwards to open into the mouth close to the opening of the parotid gland.

Teeth. The teeth are structures derived from the mucous membrane (skin) of the mouth. Each tooth consists of an extremely hard layer of enamel which is epidermal in origin, and a less hard central portion the dentine derived from the dermis. The dentine mass is hollow, its cavity being occupied by the 'pulp' of the tooth. The pulp receives blood vessels and nerve branches through the aperture at the base. Surrounding the lower part of the tooth, and filling up the folds of its surface, is a thin layer of bone, the cement. In the rabbit the aperture at the base of each tooth remains open throughout life and the tooth remains always growing. In most other mammals the base of the tooth narrows to form a root or fang, the aperture being almost obliterated. The growth of teeth in such cases ceases after certain stage.

The teeth of the rabbit do not form a continuous series. The front teeth or incisors are separated by a great gap of diastema (Fig. 8.36) from the group of grinding teeth lying in the hinder part of the mouth. Teeth corresponding to the canines of other mammals are absent in the rabbit. There are two pairs of incisors lodged in sockets (or alveoli) in the premaxillae. The anterior incisors are long and curved almost into a semicircle and the posterior incisors, lodged in alveoli immediately behind the anterior ones, are much smaller and less curved. Along the anterior surface of the anterior incisors the enamel is thick and folded so as to form a longitudinal groove. Behind and at the side it is much thinner, and hence wears away sooner, rendering the cutting edge chisel-shaped. The grinding teeth include three anterior grinders or the premolars and three posterior grinders or the molars. Each premolar is flattened from before

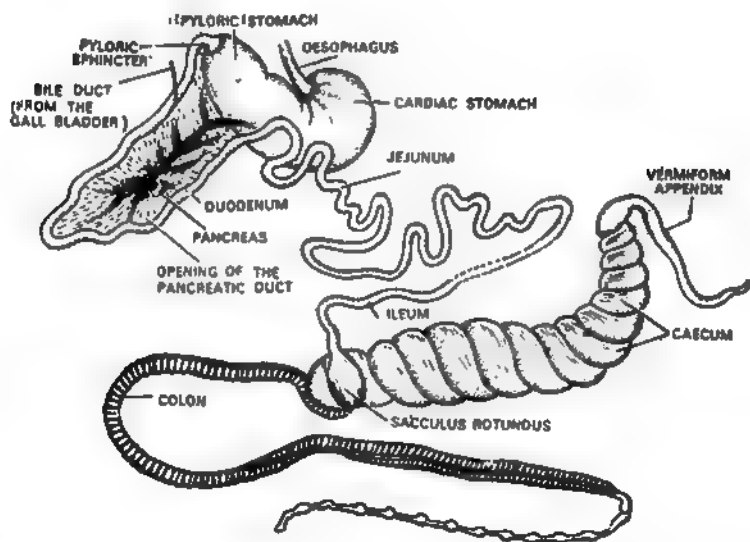


Fig. 8.37. Alimentary canal of the rabbit.

and thorax to abdomen. The lumen of the oesophagus is considerably reduced due to the folding of its lining that is made up of stratified epithelium. Immediately after its entry into the abdomen it opens into the stomach.

Stomach. The stomach is the most dilated portion of the alimentary canal and takes the form of an ovoid sac or bag which lies transversely in the abdomen. The entrance of the oesophagus has valvular arrangement called the *cardia* to prevent the regurgitation of food. The stomach towards this end is strongly rounded and is known as the *cardiac end*. The other end is somewhat narrower, called the *pyloric end* and terminates at the *pyloric constriction*. The shorter, slightly concave anterior surface of the stomach from *cardia* to *pylorus* is called the *lesser curvature*, the large convex posterior surface is the *greater curvature*. The sac-like bulge of the stomach to the left of the *cardia* is the *fundus*, the remainder of the stomach is the *body*. At the right the stomach passes into the small intestine at the *pyloric constriction* beyond which it makes an abrupt bend. In the lining of the stomach lie the gastric glands and the wall is strongly muscular.

Dorsally the stomach is suspended by the *mesogaster*. A small portion of *mesogaster* is attached to the stomach, the greater part of it forms the *greater omentum* (a large extensive sheet in other mammals) dependent upon the greater curvature of the stomach. The greater omentum is formed by reduplication of the peritoneum as such is double-walled. It passes on the stomach along the greater curvature. The spleen is enclosed in the ventral wall of the great omentum before it passes to the stomach. The portion of great omentum between spleen and stomach is the *gastrosplenic ligament*. The greater omentum is formed due to rotation of stomach. At the lesser curvature the peritoneum covering the stomach is continued as the *lesser omentum*, which passes to the liver.

The wall of stomach presents a typical structure. The outer peritoneal covering is followed by the middle muscular layer made up of an outer layer of longitudinal fibres and inner layer of circular fibres. The muscular layer is thickened at the pyloric end. Finally there is the inner layer of the mucous membrane raised and irregular

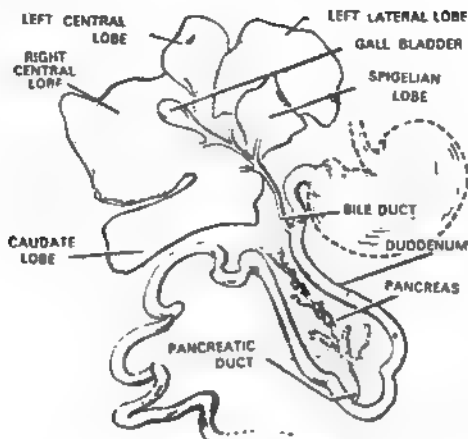


Fig. 8.39. The liver and the pancreas of the rabbit.

each villus is a lacteal vessel containing lymph (being a part of lymphatic system) and is concerned with the absorption of fat. In other histological details the small intestine of the rabbit shows little differentiations from that of the frog. The serosa, the musculature, the submucosa and the mucosa all show the same relationship. In the wall of duodenum, at the bases of the villi are special glands, the Brunner's glands, which open into simple test tube-like structures between the villi known as the crypts of Lieberkuhn. The Brunner's glands along with the crypts secrete succus entericus, and alkaline watery fluid containing mucin and also other important enzymes. In the intestine of some mammals (cat, horse, etc.) Peyer's patches present a honey combed appearance, the depressions being occupied by smooth convex lymph-follicles bordered by villi.

The small intestine is followed by the large intestine. At the junction of the two occurs a blindly ending diverticulum, the caecum, which terminates in a narrower vermiform appendix. The three way junction (between small and large intestine and the caecum) is marked by a swelling, the sacculus rotundus. The opening of ileum in the rotundus is guarded by a valve, the ileo-caecal valve by which the contents of the ileum can pass on the caecum before passing into the colon. The caecum varies in length in different mammals, and in the rabbit, whose food is almost exclusively vegetable, the caecum is large (about a foot and a half long) consisting of a series of pouch-like dilations. Terminally it narrows more or less suddenly into the vermiform appendix, which is five or six inches long. The inner surface of the caecum is papillose, and raised along the line of external constriction onto a prominent spiral fold, a quarter of an inch or more in width. The opening of the caecum into the sacculus rotundus is small and circular but that into the colon is much larger. The larger intestine beyond the caecum is called the colon, which is supported by a dorsal mesentery (mesocolon). The first part of the colon (ascending colon) is somewhat long and pursues a rather winding course. At first the wall of colon bears three longitudinal muscular bands or taeniae of colon. Between the taeniae the wall of the colon presents little sacculations, the haustra. The ascending colon is followed by a transversely running portion or transverse colon. At the left it turns abruptly as the descending colon, the terminal portion of which is called the rectum. The rectum passes to the exterior through the ring formed by the pelvic girdle and vertebral column and opens to the outside at the anus, a sphinctered opening separate from the urinogenital openings.

On the wall of the intestine are abundantly present small portions of lymphatic tissue called lymph nodules. Aggregations of lymph nodules are called Peyer's

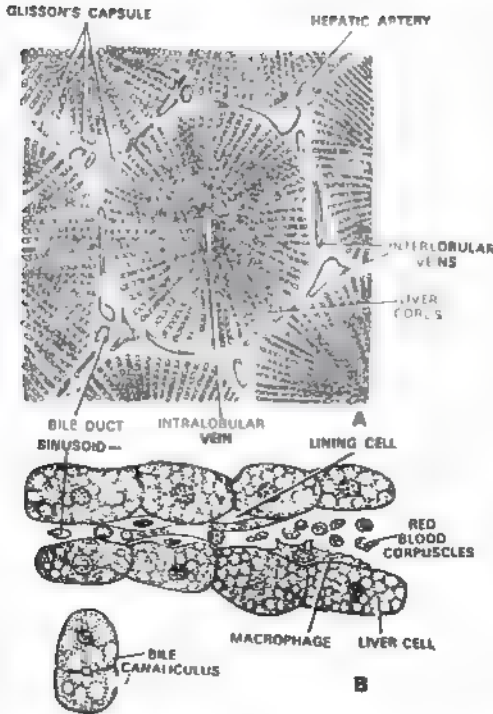


Fig. 8.40. Cross section of the liver of a mammal. **A**, showing lobules; and **B**, two hepatic cords. The two cells in the first row show a bile canaliculus enclosed between them.


patches. They occur along the entire small intestine on the side opposite to that attached to the mesentery in the form of thickened oval spots on the surface. There is a larger patch at the place of junction of sacculus rotundus and caecum.

Digestive Glands. The liver is a very large gland made up of five lobes, the right and left central, the left lateral, the caudate and Spigelian lobes. It presents a convex anterior surface fitting against the posterior surface of the diaphragm and a concave posterior surface fitting over the stomach and first part of the small intestine. The gall-bladder is large and lies between the right and left central lobes. From the gall-bladder arises the main bile duct or cystic duct which receives subsidiary ducts from the various liver lobes and opens into the rather swollen beginning of the duodenum (Fig. 8.39).

The liver is a solid glandular organ made up of hepatic lobule separated from one another by connective tissue. In some mammal such as the pig the separation is complete, but in others such as the rat or rabbit it is incomplete. Each lobule consists of a mass of polyhedral hepatic cells which are granular in appearance containing spherical nuclei. A network of blood vessels pierces the lobules there being thus, interlobular blood vessels lying in between lobules, as well as intralobular blood vessels lying in the centre of the lobules. The hepatic cells are arranged in longitudinal cords. In between the hepatic cells are spaces (intercellular spaces) which receive the

As the food passes down the duodenum it receives more water and forms a fluid emulsion called chyle, which is slowly forced by peristalsis through the long small intestine. Throughout the process enzymatic actions continue. The result is that the proteins are hydrolysed to amino-acids, the carbohydrates to glucose or similar mono-saccharide sugars and the fats to glycerols and fatty acids.

Ordinarily food is not absorbed in the buccal cavity or the stomach (only drugs and alcohol may be absorbed). Major absorption takes place in the jejunum and ileum, where the food passes through the walls into the capillary blood vessels. The digested carbohydrates as monosaccharide sugar and proteins (as amino-acid) are collected by branches of the hepatic portal vein and are conveyed to the liver, which acts as a regulating mechanism. Only the required amount of blood sugar is allowed to enter the blood leaving the liver by hepatic vein. Excess of sugar is transformed into animal starch or glycogen and stored till the amount of sugar in blood falls. Under such a circumstance the glycogen is turned once more into glucose and released. Liver thus acts as a store house of carbohydrates, but proteins cannot be stored. The amino-acids pass into the blood stream in suitable quantities, but the excess of amino-acids is subjected to the process of *delamination* in the liver forming relatively harmless substance *urea*, which is excreted by the kidneys, and into other products which can be transformed into glucose. The fatty acids and glycerols (formed by fats of the food) pass into the lymph vessels (lacteals) directly as minute fat globules. The lymph vessels therefore contain a whitish fat emulsion. This enters the blood stream through ducts (thoracic and right lymphatic) connecting lymph vessels with the blood vessels. Some authors believe that fat globules are picked by cells of the epithelium covering the villi and some believe that some digested fat enters blood capillaries of the villi. The carbohydrates and fats so absorbed are used as sources of energy for vital activities and the proteins are used for building up new protoplasm. After delamination proteins are used for building up new protoplasm. After delamination proteins also produce energy-containing substances.

By the time the digested products are absorbed, the fluid content of the alimentary canal passes into the colon. Here the water is absorbed by the colon. All this water comes from the body tissue and organs and if passed out, the water will be lost. But water conservation is a vital problem which is solved by the absorption of water in the colon. The result is that by the time the food residuum reaches the rectum it is semisolid and forms the *faeces* which are egested or extruded at intervals through the .

CIRCULATORY SYSTEM

The mammalian circulatory system is more complex because the adult pattern is reached only after an elaborate metamorphosis of the originally complex system of the early embryo. The heart appears as a simple cardiac tube and differentiates into original four chambers, sinus venosus, atrium, ventricle and bulbus cordis. The atrium divides into two, right and left, auricles by an interauricular septum, and so does the ventricle (by an interventricular septum). The bulbus cordis and ventral aorta split longitudinally forming two aortae, the carotico-systemic aorta and the pulmonary aorta, arising directly and separately from the ventricles and not from a common trunk as in lower vertebrates. With further development the sinus also becomes incorporated in the wall of the right auricle, leaving a four chambered adult heart comprising two auricles and two ventricles.

Heart. The ovoid or pear-shaped heart lies in the centre of the anterior part of the thorax, completely enclosed by the pericardium. The greater portion of the heart consists of the two ventricles, which constitute a firm thick-walled cone having a posterior pointed apex and a broad anterior base. This cone consists of two completely separated ventricles (right and left) the division between them being marked externally by an indistinct groove extending from the left side of the base obliquely to the right and terminating to the right of the apex. The groove contains the branches of the coronary artery and vein which ramify over the surface of the ventricles. Anterior to the base of each ventricle is a much smaller generally dark coloured chamber, the

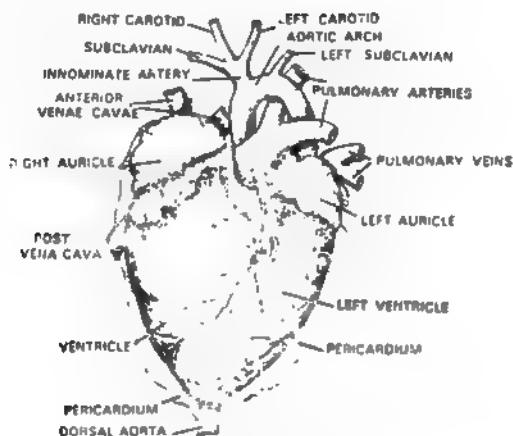


Fig. 8.42. Ventral view of the heart of the rabbit

auricle. Each auricle in a contracted stage looks like a lobe, the **auricular appendage**, projecting medially and slightly posteriorly over the ventricle. Extending anteriorly from the middle of the base of the ventricles forward between the two auricles is a large artery, the **pulmonary artery**, which arches to the left. Dorsal to this is another arterial trunk, the **aorta**. Both these represent the split ventral aorta. The two trunks are generally embedded in fat. On the dorsal side there is no sinus venosus as a distinct chamber, the bases of the great veins directly enter the auricle. In the rabbit the right and left anterior venae cavae both exist and open separately just anterior to the opening of the posterior vena cava. In other mammals (e.g. cat) the anterior vena cava of the left side degenerates and the blood of that side is passed to the right anterior vena

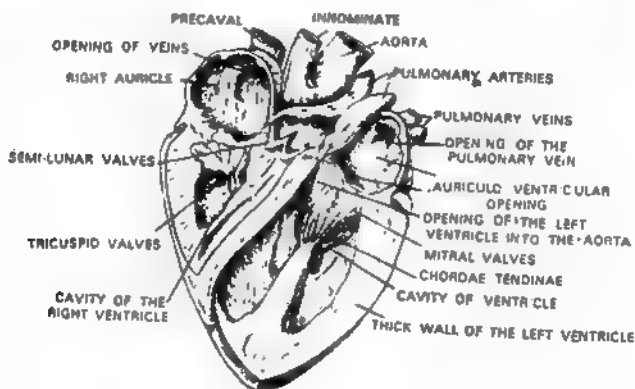


Fig. 8.43. Internal structure of the heart of the rabbit. This figure shows only one (right) pre-caval entering the right auricle, the other is lost. In the rabbit, all three venae cavae open separately

cava through a newly formed left brachiocephalic vein. Consequently there are only two openings (Fig. 8.43) in the right auricle, those of right anterior vena cava and the postcaval. The left anterior vena cava persists only as the coronary vein.

Arteries. From the base of the ventricles directly arise the two aortae, the **systemic aorta** from the left and the **pulmonary aorta** from the right ventricle. Because the *bulbus cordis* becomes twisted before splitting, the bases of the aortae are twisted around one another. The systemic aorta is dorsal to the pulmonary aorta and forms a curve, known as the arch of the aorta, to the left. From the arch of the aorta spring the large arteries of the neck, head and forelimbs. These are three in number. Beginning at the right they are the **brachiocephalic** or **innominate**, the **left common carotid** and the **left subclavian**.

The pulmonary aorta arising from the base of the right ventricle runs forward between the auricles and finally curves to the left. At the turn it divides into two right and left **pulmonary arteries**, each of which bends dorsally and runs to the lung of its side. Where the pulmonary aorta passes beneath the arch of the systemic aorta a solid cord, the **ductus arteriosus**, connects the two (Fig. 8.43).

From the systemic arch and the dorsal aorta arise the main arteries of the body. The first artery to arise from the arch is the **brachiocephalic** or **innominate**. Usually from this arise the **right** and **left common carotid**, but this is not invariable and the left common carotid may arise directly from the aortic arch. The brachiocephalic artery is the remnant of the ventral aorta that has become connected with the systemic which for this reason is often called the **carotico-systemic arch**. The presence of the neck introduces certain complications in the course of carotid arteries. The common carotid becomes quite long and traverses the neck before it divides into the **internal** and **external arteries**. The **right subclavian** arises from the base of the brachiocephalic in the rabbit (or from the base of the right common carotid). The **left subclavian** originates independently from the left side of the arch (Fig. 8.44).

From the posterior surface of the subclavian arises the **internal mammary artery** which follows the vein of the same name along the ventral chest wall. At the same level from the posterior surface of the subclavian, practically in common with the preceding, the **supreme intercostal artery** arises. It runs posteriorly on the dorsal wall of the thorax and gives off the first **intercostal arteries**. On its anterior surface at about the same level as these the subclavian artery gives rise to the **vertebral artery** which passes immediately dorsally towards the cervical vertebrae, where it enters the vertebralarterial canal, and to the **superficial cervical artery** which ascends in the lateral part of the neck, supplying various muscles of the region. After giving off these branches the subclavian passes in front of the first rib into the fore-limb as the **brachial artery**, lying between the two stout nerves of the **brachial plexus**. It gives many small branches to the shoulder and muscles of the region. Of these the **thoracoacromial artery** supplies the pectoral and deltoid muscles, the **thoracic artery** posteriorly supplying serratus muscle and then as the **external mammary artery** passes to the under surface of the skin of the lateral abdominal wall being especially conspicuous in females, and the **subscapular** supplying muscles of the scapular region.

Dorsal Aorta. After it has passed in diaphragm, the **dorsal aorta** (abdominal aorta of some authors) runs against the dorsal wall in the median dorsal line and gives off several branches as it proceeds backwards. These branches consist of unpaired **median visceral branches** to the digestive tract, paired **lateral visceral branches** to the kidneys and reproductive organs, and paired **somatic branches** to the body wall.

Shortly posterior to the diaphragm, the aorta gives rise to two large unpaired visceral arteries, the **coeliac** and the **superior mesenteric**, one-half inch posterior to the coeliac. The coeliac artery near its origin gives rise to the small **inferior phrenic artery** to the diaphragm. Beyond this point arises the **lienogastric artery** from its posterior surface. This vessel passes in the mesogaster to the spleen. During its course it provides the short **gastric arteries** to the left end of the stomach, and the **splenic branches** to the spleen. Beyond the spleen it branches into the omentum. At about the middle of the spleen a large branch the **left gastroepiploic artery** arises from the spleen and passes to the greater curvature of the stomach. Beyond the splenic the coeliac artery passes to the lesser curvature of the stomach. Here it gives off a group of vessels, the **left gastric**

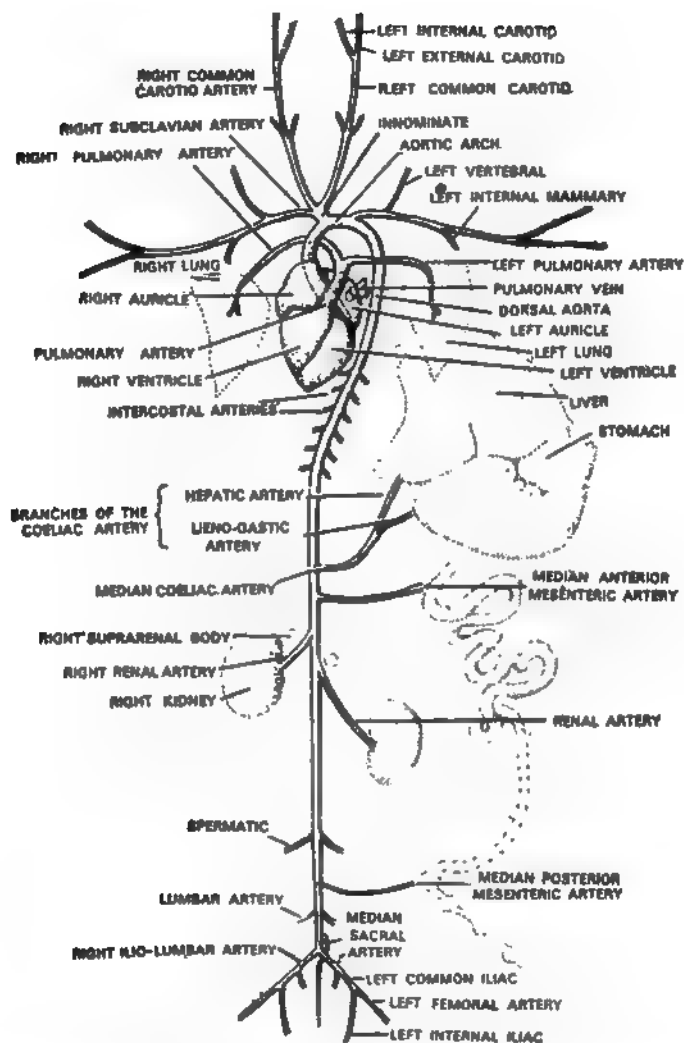


Fig. 8.44. The arterial system of the rabbit.

(or coronary) arteries which radiate to the wall of the stomach on both sides of the lesser curvature, and also branches to the oesophagus. Shortly beyond the point of origin of the lienogastic the coeliac artery is known as the **hepatic artery** going to the liver. This gives rise to a **gastroduodenal artery** which runs to the pyloric region of the stomach giving branches to it and to the pancreas and first part of the duodenum, and the right **gastroepiploic artery** which returns to the stomach by way of the great

omentum. The hepatic artery now passes to the dorsal side of the pylorus and enters the hepatoduodenal ligament. After giving off the small right gastric artery to the pylorus it proceeds to the liver, lying to the right of the bile duct.

The **anterior mesenteric artery** is the chief artery of the intestine and has many complicated branches. In the rabbit these branches follow, for the most part, the branches of the hepatic portal vein. It runs alongside the superior mesenteric vein. The first branch is the small middle coeliac artery, arising from the ventral wall of the superior mesenteric and passing to the transverse colon and beginning of the descending colon. At the same level but from the dorsal side arises the **posterior pancreaticoduodenal artery** which passes to the duodenal loop and pancreas. The **superior mesenteric artery** then forks into the **intestinal artery**, which runs in the mesentery of the small intestine and gives off numerous branches ventrally into the intestine, and into the large **ileo-caeco-colic artery**. This last gives many branches to the ileum, the caecum, appendix, and the ascending colon.

Next arise the paired **renal arteries** from the aorta, the right one arising just behind the anterior mesenteric and the left a little farther back. Each gives a small branch to the muscles of the back and then runs outwards to the kidney of its side. In the male a pair of **spermatic arteries** arise about a couple of inches behind the left renal artery and run backwards and outwards along the dorsal surface of the abdomen to enter the equidistyles at their anterior ends. In the female the **ovarian arteries** arise in the same position as the spermatic and run outwards and slightly forwards to the ovaries. About an inch in front of its division into the common iliacs the dorsal aorta gives rise to a median vessel, the **posterior mesenteric artery**, which supplies the hinder part of the rectum. In the same region from the dorsal surface of the aorta arise small **median lumbar arteries**, which soon divide into right and left branches supplying the body walls. Shortly before the aorta divides it gives a small vessel, the **median sacral artery**, that runs along the ventral surface of the sacrum to the tail. Some people regard it as the posterior continuation of the aorta. At this point the aorta bifurcates into two, the **right and left common iliac arteries**. Each runs backwards and outwards to the hind limbs along which it is continued as the **femoral artery**. Before entering the limb each gives rise to three important branches. The **ilio-lumbar artery** runs outwards along the posterior part of the dorsal wall of the abdomen. The **internal iliac artery** runs backwards along the dorsal wall of the pelvic cavity. The **venal artery** is a small branch which runs backwards to the bladder. In the female it also supplies the uterus.

Veins. There are three sets of veins communicating with each other through capillaries and containing different kinds of blood, (i) there are three systemic veins, namely, the two **precavae** and one **postcaval**, bringing venous blood from all parts of the body to the right auricle, (ii) the **hepatic portal system** collecting blood from the walls of the alimentary canal, pancreas and spleen and carrying it to the liver, and (iii) the **pulmonary system** bringing arterial blood from the lungs to the left auricle.

Right Anterior Vena cava. It is formed by the union of jugular and subclavian veins immediately in front of the first rib. At the point of entrance into the right auricle it receives from behind the **azygos cardinal vein**, a median vein which runs forwards in the mid-dorsal line of thorax lying close to the vertebral column along the right side of the aorta. It receives vein from the posterior seven or eight intercostal spaces (the **intercostal veins**) from both sides of the body. Entering the precaval immediately anterior the entrance of the azygos is the **supreme intercostal vein**, the first of the series of intercostal veins. Shortly anterior to this the **internal mammary veins** enter the precaval. This vein ascends on the internal surface of the chest very near the midventral line. It continues posteriorly on the abdominal wall as the **superior epigastric vein**. The next tributary of the precaval is the **vertebral vein**. It enters the medial side of the precaval at about the same level as the internal mammary joins the lateral side. It may be traced deep dorsally to the cervical vertebrae from which it emerges receiving a **costocervical** tributary from the neck. Beyond this point the precaval receives the large **subclavian vein** from the fore-limb. It passes between the first and second ribs into the axilla and is then known as the **brachial** (axillary of some authors) vein.

At the point of entrance of subclavian the precaval vein receives from the neck the

highly variable, it may enter the precaval after the latter has received the subclavian, but it usually enters with the external jugular. The precaval vein may thus be said to be formed by the union of the subclavian, external jugular, and internal jugular veins. Shortly anterior to its union with the subclavian it receives the **transverse scapular vein** from the ventral end of the shoulder and near the same level has a cross-connection (**transverse jugular vein**) with its fellow of the opposite side (this union is very delicate and is usually destroyed in dissections). Along the neck it receives various small tributaries from muscles and about one inch posterior to the angle of the jaws is seen to be formed by the union of two veins, the **anterior and posterior facial veins**. The anterior facial vein proceeds to the angle of the jaws where it is seen to be formed by the union of veins from the anterior part of the face and jaws. The posterior facial vein passes to the parotid gland where it receives smaller branches bringing blood from the back of the ear and the head. The **internal jugular vein** is a small vessel collecting blood from the brain. It runs alongside the trachea throughout the length of the neck and opens into the right external jugular vein close to its union with the subclavian.

The **left anterior vena cava** is identical in its course and branches, except that there is no azygos vein on the left side.

The **posterior vena cava** is a large median vein that runs from the hinder end of the abdomen to the heart. It lies close to the vertebral column and to the right (or left) of the aorta. Anteriorly it leaves the abdominal wall and becomes embedded in the dorsal surface of the liver, beyond which it enters the thorax through an aperture in the central tendon of the diaphragm. It runs forward and enters in the right auricle. During its course it receives several branches. As the postcaval passes through the diaphragm it receives the small **phrenic veins** draining the diaphragm. From the liver the postcaval receives the **hepatic veins**. There are four chief hepatic veins that open into the postcaval while it is embedded in it. From the kidneys the blood is conducted to the postcaval by a pair of large renal veins. Of these the right is shorter and about three-quarter of an inch in front of the left. Each renal vein receives a small vein from the corresponding adrenal body and a large one from the dorsal wall of the abdomen. Near the hinder end of the abdomen a pair of the **spermatic veins** in the male (or **ovarian vein** in the female) open into the vena cava. Frequently the left one opens into the renal vein or the **ilio-lumbar vein**, which are paired veins returning blood from the hinder part of the walls of the abdomen. They open into the vena cava about the level of the anterior border of the thigh. The blood from the hind-limbs is returned by a pair of **external iliac veins**. These are large veins opening into the vena cava at the hinder end of the abdomen, a little in front of the pubic symphysis. They receive small veins from the bladder and in the female also from the uterus. The external iliacs are direct continuations of the **femoral veins**, which lie along the inner or preaxial borders of the thighs of the two sides. From the back of thigh the blood is returned by the **internal iliac vein**. Each of them runs forward through the pelvic cavity and unites its fellow from the opposite side about half an inch behind the external iliacs to form the posterior end of the postcaval.

Portal System. The portal system in the rabbit consists of only the **hepatic portal veins** collecting blood from the whole length of the alimentary canal and from the spleen and pancreas. This is one set of blood vessels that has not undergone any evolutionary change in the vertebrate series. The veins from different parts of the alimentary canal converge to form one trunk the **portal vein**, which runs alongside the posterior vena cava and divides into two branches before entering into the liver. There are many vessels forming the hepatic portal vein but here only four main trunks have been described. Of these the first is the **lienogastric vein** that returns blood from the walls of the stomach (**gastric** or **gastroepiploic**) and the spleen (**splenic**). From the duodenum the blood is returned by the **duodenal vein** (or **pancreatico-duodenal**). Blood vessels from the whole length of the small intestine, and from caecum, the colon and the greater part of the whole length of the small intestine, and from caecum, the colon and the greater part of the rectum unite to form the **anterior mesenteric vein** of the portal vein. The **posterior mesenteric vein** lies in the mesorectum or the hind-most part

¹ Some authors call it simply "portal veins," since there is only one portal system in mammals.

of the mesentery and returns blood from the terminal portion of the rectum.

Pulmonary Veins. There are several pulmonary veins in the rabbit. They convey the aerated blood from the lungs into the left auricle. They lie on either side of the postcaval. Those of the right side passing dorsal to the postcaval and those of the left side pass to the dorsal side of the left precaval.

Course of Circulation. There are only two kinds of chambers in the mammalian heart, namely, auricles and ventricles. Each of these is completely divided into two

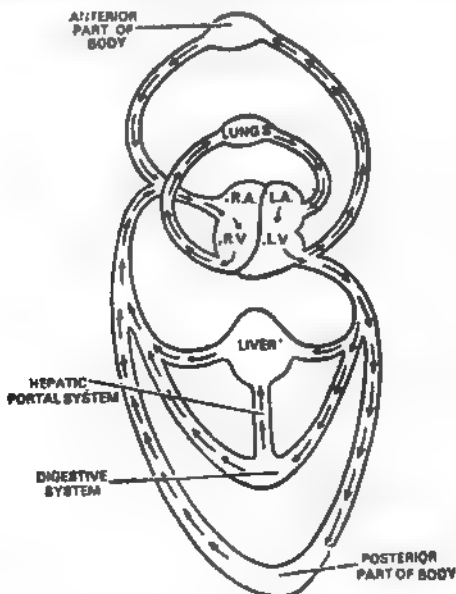


Fig. 8.46. Course of circulation in a mammal.

compartments, right and left by the formation of septa in the centre of the originally single chamber. The division of the auricle begins with the Amphibia, while that of ventricle in reptiles and is completed in crocodiles, birds and mammals. The conus arteriosus has vanished in reptiles leaving as remnants the semilunar valves at the bases of the great arteries. The sinus venosus has disappeared in birds and mammals and is represented in the latter by a small spot in the wall of the auricle. The ventral aorta is split into two trunks (as in birds but unlike reptiles in which it splits into three). Of these the pulmonary artery leaves the right ventricle, and aorta the left ventricle. All the main veins open directly into the right auricle and the pulmonary veins into the left auricle. The right half of the heart is venous and the left arterial and owing to the completion of the interventricular septum there is no mixing of arterial and venous blood in the heart; but a *complete and perfect double circulation* (Fig. 8.45) is maintained. The venous blood passes from the right auricle to the right ventricle and out through the pulmonary artery to the lungs for aeration. The arterial blood returns by way of the pulmonary veins to the left auricle, passes into the left ventricle and out of the aorta to the different parts of the body.

RESPIRATORY SYSTEM

The respiratory mechanism of mammals is more complicated. The lungs are the sole

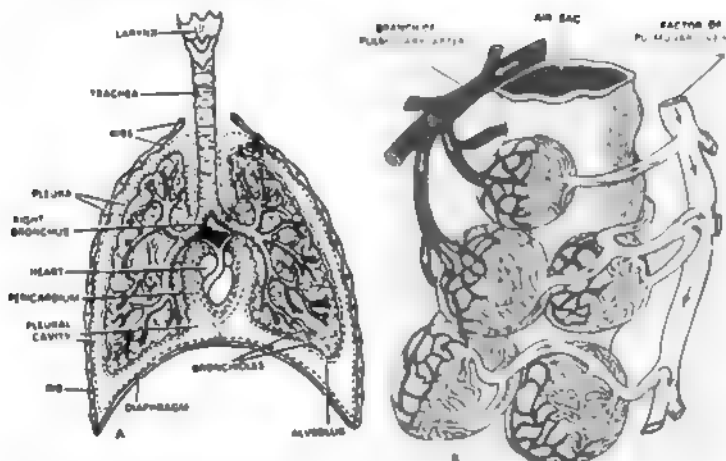


Fig. 8.49. A, median longitudinal section through the thorax of the rabbit, B, figure showing the arrangement of blood vessels in alveoli.

ventral margin projects the cartilaginous flap-like **epiglottis** which serves to prevent food entering the glottis during swallowing. The ventral wall of the larynx is supported by a shield-shaped **thyroid cartilage**. A short distance posterior to this is the **cricoid cartilage** which forms a ring around the larynx. The dorsal rim of the glottis is supported by a pair of projecting **arytenoid cartilages**. At the apices of the arytenoids are situated a pair of small nodules the **cartilages of Santorini**. Extending between the thyroid and arytenoid cartilages are two pairs of membranous folds, the **vocal cord**. Of these the anterior pair is that of the **false vocal cords** which may be absent in some. The posterior pair is known as the **true vocal cords**. The vocal cords are folds of the lateral wall of the larynx, and close the glottis except for a slit between their free edges, and it is through this gap that air enters during the respiratory movements.

Trachea. From the larynx the **trachea** or **windpipe** proceeds posteriorly. Internally the trachea is lined by ciliated epithelium. Its walls are stiffened by cartilaginous **tracheal rings**, which are incomplete dorsally leaving a soft strip into which the oesophagus fits. The function of these cartilages is to prevent the trachea from collapsing and to allow a free passage of air from the pharynx to the lung. The trachea runs through the length of the neck and on emerging it divides into **right and left bronchi**, which have the same structure as the trachea. Each bronchus passes into the lung of its side, and divides and sub-divides into finer branches called **bronchioles**. The ultimate branches terminate in small dilated air-sacs bearing **alveoli**. Each alveolus is surrounded by a network of fine capillaries in connection with the pulmonary artery and vein of the lung.

The right and left **lungs** are spongy masses of tissue lying in the pleural cavities of the thorax. The left lung is a soft spongy organ divided into three lobes, a smaller **anterior**, larger **middle** and **posterior lobes**. The anterior lobe is very small in the rabbit and the large posterior lobe fits on the convex surface of the diaphragm. The right lung is somewhat larger than the left. It is divided into **anterior (azygos lobe)**, **middle** and **posterior lobes**. The large posterior lobe is subdivided into lobules a **medial (posterior azygos lobe)** and **lateral lobe**.

Ventilation of Lungs. The air gets in and out of the lung by the movement of the diaphragm and the ribs. The muscular diaphragm in the position of rest is domeshaped, the curvature of the dome is directed towards the anterior side (thoracic cavity). The ribs that are embedded in the wall of the thorax are movable because of the presence of

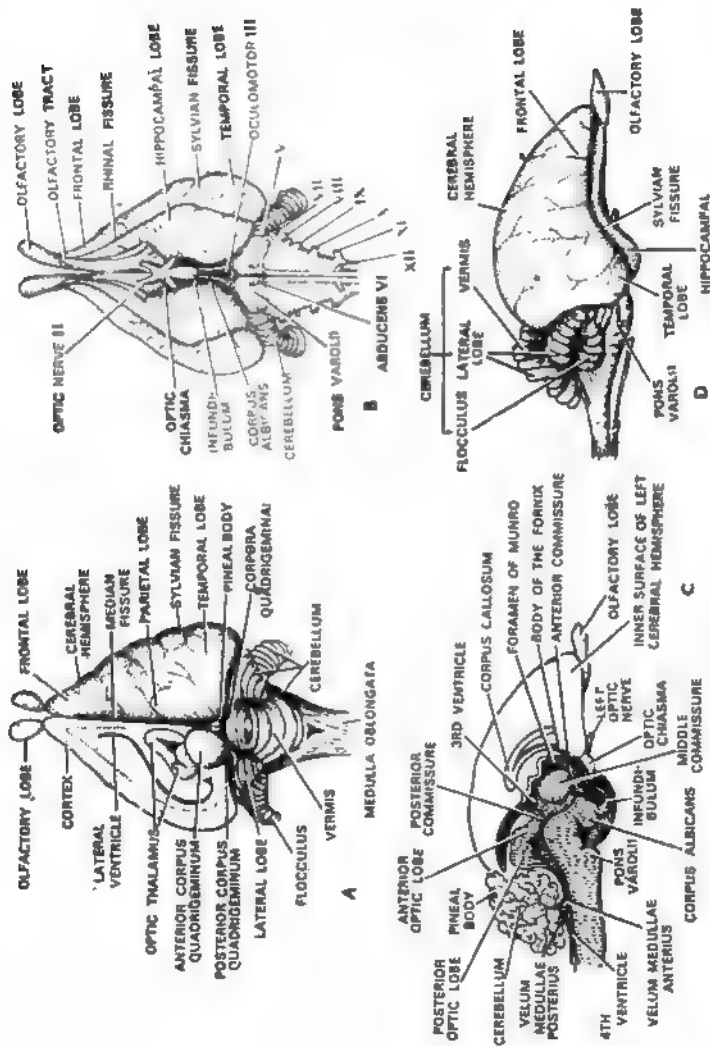


Fig. 8.52. Brain of the rabbit. A, dorsal view with a portion of the cerebellum removed; B, ventral view; C, median sagittal section; and D, lateral view.

form the **cerebellum** while the posterior part of the roof is thin, and variously folded and inpushed to give rise to the **posterior choroid plexus**. The **cerebellum** in the rabbit is again very largely developed. It is made up of many regions—a median lobe called the **vermis**, two lateral lobes, each of which terminates, laterally in the **flocculus**. Ventrally there is the much thickened **medulla oblongata**. Extending transversely across the under side of the medulla and connecting the two sides of the cerebellum is a tract of nerve fibres called **pons Varolii**.

The hind border of the optic lobes is connected with the cerebellum by a thin transparent membrane called the **velum medullae anterioris** (valve of Vieussens) that also roofs over the fourth ventricle. Another thin transparent membrane the **velum medullae posterioris** forms the roof of the posterior part of the fourth ventricle. In front it is covered by the cerebellum.

Seen from the ventral surface the medulla is broad in front and gradually narrows behind. It is marked by a median ventral fissure, bordered by two narrow bands, the ventral **pyramids**. At the outer sides of the pyramids, immediately behind the pons Varoli are a pair of oblong patches of transverse nerve fibres, the **corpora trapezoides**.

Ventricles. Within the cerebral hemispheres lie the spaces called the **lateral ventricles**. In the brain of the rabbit the lateral ventricles are reduced and anteriorly each extends as a narrow vertical slit, the **anterior cornu**. Posteriorly the lateral ventricle curves backwards and inwards towards the hind end of the hemisphere as the **posterior cornu**. From its outer side a little behind the middle of the hemisphere a **descending cornu** runs outwards and downwards ending opposite the infundibulum. The lateral ventricles communicate posteriorly with the **third ventricle** through the **foramen of Monro**. The third ventricle is a narrow vertical cleft between the optic thalami and passes backwards opening into the very narrow **iter**. The cavities of the optic or **optocoels** also open into the iter as in other vertebrates. The iter finally leads into the **fourth ventricle**, the cavity of the hind-brain. It is moderately wide from side to side but shallow from above downwards. It has a very thin roof but thick floor and sides.

Cranial Nerves. Twelve pairs of cranial nerves arise from the brain of the rabbit. The **olfactory nerve** arises by many roots from ventral surface of the anterior end of the olfactory lobe. Lying immediately in front of the infundibulum there is **optic chiasma** from the anterior border of which arise the second pair of **optic nerves**, which run forwards, curve outwards and enter the eye. The third pair of nerves, the **oculomotor**, is small and arises from the inner border of the crura cerebri close to the middle line. It innervates inferior oblique and those of the rectus muscles of the eye. It also innervates levator palpebrae that lifts the eyelid, and the iris and ciliary muscles. The fourth or **pathetic** is again small and arises from the dorsal surface of the valve Vieussens, close to the middle line, and just behind the optic lobes. It then runs round the sides of the brain to the ventral surface running between the cerebellum and the optic lobes; it finally enters the orbit and supplies the superior oblique muscle of the eyeball. The fifth nerve or the **trigeminal** is very large, and arises by two closely apposed roots from the side of the hinder border of the pons Varoli. Of the two roots the inner smaller one is motor and the larger outer one is sensory in function. Its branches and mode of distribution is similar to that of the fifth of other vertebrates. The sixth or **abducens** nerve is very slender and arises from the ventral surface of the medulla, close to the middle line immediately behind the pons Varoli, it supplies the lateral and external rectus muscles and also nictitating membrane. The seventh or **facial nerve** takes its origin from the outer side of the anterior end of the corpus trapezoidium immediately behind the fifth nerve. The **auditory nerve** is large and arises from the side of the medulla, immediately behind and to the outer side of the facial nerve. The ninth (**glossopharyngeal**) and tenth (**vagus**) arise close together by many slender rootlets from the side of the medulla close behind, and a little above the root of the auditory nerve. The fate and distribution of all these nerves is similar to those of other vertebrates. The eleventh or **spinal accessory nerve** arises from the side of the medulla and the spinal cord by about ten rootlets the most anterior of which is just behind the pneumogastric and the hindmost is as far back as the fifth spinal nerve. The twelfth or **hypoglossal nerve** also arises by a number of rootlets from the ventral surface of the

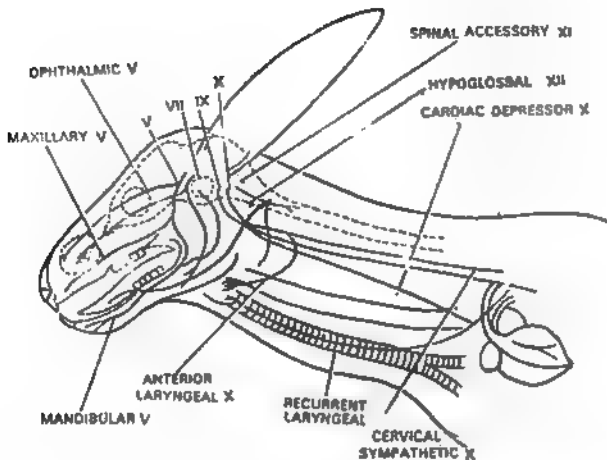


Fig. 8.53. Cranial nerves of the rabbit

medulla close to the middle line, and to the outer side of the ventral pyramid. The eleventh and twelfth both are motor nerves, but eleventh includes both somatic and visceral fibres and twelfth contains purely somatic motor fibres. The eleventh innervates pharyngeal, laryngeal and cervical muscles and thoracic and abdominal viscera while the twelfth supplies the tongue muscles.

Spinal Cord. The spinal cord lies in the neural canal. It is loosely enclosed in a tough membrane the **dura mater**, from which strands pass to the walls of the neural canal. The space between the dura mater and the spinal cord is the **subdural space**. The spinal cord is closely invested by a membrane called the **pia mater**. Between these two is another delicate membrane, the **arachnoid**, which along with the pia mater corresponds to the pia mater of lower vertebrates. The spaces around and between these membranes are filled in life with the **cerebrospinal fluid**, which is modified lymph. The structure of the spinal cord is similar to that of other vertebrates. There is a **median dorsal fissure (sulcus)** in the dorsal line, a **median ventral fissure** in the mid-ventral line. Lateral to the dorsal median sulcus is the **dorsolateral sulcus** along which the dorsal roots enter the cord. The region between the median dorsal and dorsolateral sulci is called **dorsal funiculus**. The region of the cord between the dorsolateral sulcus and the line along which the ventral roots emerge is the **lateral funiculus**. Between this and the ventral median tissue is the **ventral funiculus**.

Nerves of the Neck The interposition of the neck between the thorax and head had brought about some complications in the course of some nerves. Certain branches of the tenth nerve show more complications than others that simply elongate. In the frog (neck-less animal) all aortic arches are close to the larynx but in the mammals (animals with necks) the arches 4-6 occupy more posterior positions and the common carotids elongate. Now the posterior nerve to the larynx in a mammal loops on the right side around the subclavian artery and on the left, around the ductus arteriosus. The nerve branch, as such, arises at its normal position on the main trunk of the vagus and recurves around the subclavian artery or the ductus arteriosus and elongates to run through the neck alongside the trachea to the larynx. This is the **recurrent laryngeal nerve**. The nerve has been described here because of its curious course. Other nerves that pass through the neck are given below.

The eleventh or **spinal accessory nerve** leaves the skull by the foramen lacerum posterius, along with the glossopharyngeal and pneumogastric nerves, and takes a

lateral cutaneous a stout trunk passing to the thigh. A slender **genitofemoral nerve** also arises from the fourth lumbar and innervates the abdominal wall of and adjacent to the inguinal region. The fifth lumbar sends a branch to the lateral cutaneous of the fourth and with the sixth forms a stout **femoral nerve** which enters the medial surface of the thigh along with femoral artery and vein. The connecting band between the sixth and seventh gives off the slender **obturator nerve**. The seventh lumbar together with the first sacral forms the stout **sciatic nerve**, which turns dorsally passing ilium and the vertebral column. The **puddental** and **posterior cutaneous** are other nerves arising from the sacral plexus. The pudental innervates the rectum and the posterior cutaneous supplies the muscles of the region. The fourth sacral passes laterally and then turns posteriorly to the rectum.

Sympathetic System. The sympathetic system in the rabbit consists chiefly of a paired ganglionated cord in the mid-dorsal region of the body cavity. These are connected with the spinal and cranial nerves by communicating branches and with the viscera, glands, blood vessels, etc. by means of branches, networks, or plexi, and ganglia. The relations of the sympathetic nerves are essentially similar to those occurring in other vertebrates. Each sympathetic nerve passes backwards along the neck close to the vagus and alongside the carotid artery. In the neck region it enlarges forming anterior and posterior **cervical ganglia**. In the thorax it runs just beneath the head of the ribs, having a ganglion in each intercostal space. In the abdomen it runs close to the centra of the vertebrae enlarging at intervals forming ganglia. Communicating branches (**rami-communicantes**) arise from each ganglion and meet the adjacent spinal immediately on its emergence from the intervertebral foramen. Other branches from the ganglia go to the blood vessels. Some branches in the thorax and abdomen are connected with plexi from which nerves pass to the heart and the abdominal viscera.

In the thorax the **greater splanchnic nerve** from the sympathetic trunk on each side and passes obliquely toward the diaphragm. The splanchnic nerves pass to either side of the cura (muscular cords fastening the diaphragm to the lumbar vertebrae) of the diaphragm into the abdominal cavity. In the abdomen two prominent sympathetic ganglia are situated on the superior mesenteric. These are the **coeliac** and **superior mesenteric ganglia**, lying just behind the coeliac. From these ganglia numerous branches run off to the abdominal viscera. These ganglia and nerves form what is known as the **coeliac plexus**.

SENSE ORGANS

Taste and Smell. The **taste-buds** are located on the tongue and enable the animal to detect the taste of dissolved material. The nasal cavities are long divided into the right and left cavities or **fossae** by a perpendicular **internasal septum** made up of cartilage anteriorly and thin bone posteriorly. The lateral and posterior walls of the nasal fossa are occupied by delicate scroiled and folded bones the **turbinals** or **conchae**. These are divisible into three parts. (i) the **interior concha** (**maxillitorbinal**) much folded and located on a separate small bone of the skull, (ii) the **middle concha** (**nasoturbin**), a long single fold dorsal to the preceding and dependent from the nasal bone, and (iii) the **superior concha** (**ethmoturbin**) part of ethmoid bone. The spaces enclosed by the bony folds are known as the **ethmoid cells**. The folds are covered by olfactory membranes containing sensory cells connected to the olfactory bulbs by nerve fibres running through the cribriform plate. Definite passages known as the **meatuses** of the nose run between the conchae and conduct the air to the nasopharynx.

Sight There are two mobile eyelids, the upper and lower. The **levator palpebrae superioris** is a thin sheet of muscle extending into the upper eyelid which it raises. A similar sheet of muscle, the **depressor palpebrae inferioris**, runs into the lower eyelid. Other muscles that bind the eyeball to the orbit are similar to those of other vertebrates. At their margin the eyelids bear scanty eyelashes. Within the eyelids lies the third eye lid or **nictitating membrane**, which is a hairless fold of opaque white skin, and can be pulled across the eyeball from the anterior angle or **canthus**.

cavity of the vitreous humour containing the gelatinous vitreous humour and between the lens and the cornea is the smaller **anterior chamber** filled by the aqueous humour.

Ear. The ear of mammals consists of three parts, the **external**, the **middle** and the **internal ear**. The external ear includes the **pinna** or **auricle** and the **external auditory meatus** leading into the interior of the **bullae**. The **pinnae** are large trumpet-like structures and freely movable. Each is folded longitudinally, and is supported by cartilage at its base, where it surrounds the external auditory meatus.

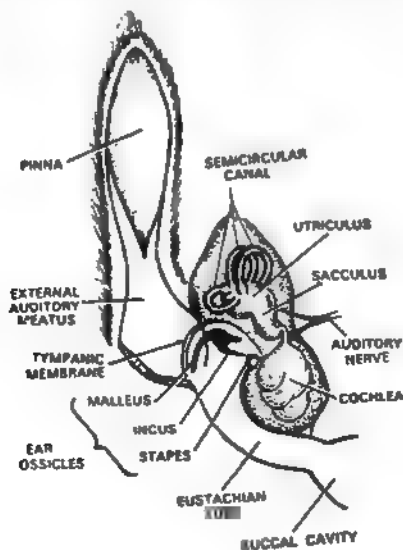


Fig. 8.99. The auditory apparatus of the rabbit.

The **middle ear** is situated inside the **tympanic bulla**, which encloses a large **tympanic cavity**. In the lateral wall of this cavity is a ring-like elevation of bone across which is stretched a delicate membrane, the **tympanic membrane** (eardrum). It has a nearly vertical position. Extending towards the tympanic membrane from the medial wall is a short calcareous process which supports the **chorda tympani** branch of the facial nerve as it crosses from the facial to the tympanic membrane. Anterior to the tympanic membrane is a depression in which are lodged the three little ear bones, the **malleus**, the **incus** and the **stapes**. They are connected with each other by definite articulations (as in other joints) whilst the malleus is attached to the tympanic membrane and the stapes to the fenestra ovalis. A small **tensor tympanic** muscle maintains the tension of the eardrum. It runs from the wall of the tympanic cavity to become inserted in the periosteum of the malleus. These bones transfer the vibrations received by the eardrum to the inner ear through the foramen ovale.

The **internal ear** in the mammals is enclosed in the channels in the petrous bone, consisting of cochlea, the semicircular canals, and the vestibule or connecting chamber. These together constitute the **bony labyrinth**. The internal ear proper or the **membranous labyrinth** is contained in the bony labyrinth. Its parts are, the **sacculus** and **utricle** enclosed in the vestibule, the **semicircular canals** arising from the utricle and situated inside the bony semicircular channels; and the **cochlear duct** arising from the sacculus and enclosed in the cochlea. The cochlear duct is a new structure characteristic of mammals although it begins to appear in birds. It is an

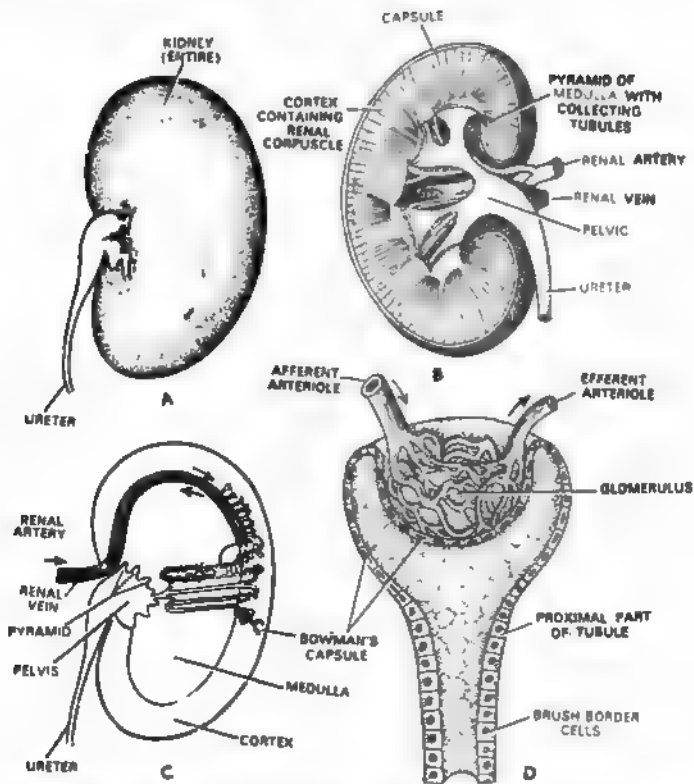


Fig. 8.61. Kidney of rabbit. A, Entire; B, Longitudinal section; C, Diagrammatic representation of the main regions; D, Sagittal half of a Malpighian body.

cavity of the kidneys called *sinus* within the hilus. The pelvis receives the urine from the apertures on the renal papilla. The collecting tubules and the renal papilla form a *pyramid* of which there is only one in the rabbit although in man there are twelve.

Metanephros. The *metanephros* is a novelty of the amniotes. In some amphibians, however, transitional condition between *mesonephros* and *metanephros* occurs in the form of combined *mesonephros* and *metanephros* (the *opisthonephros*). As the posterior portion of *mesonephros* develops the anterior tubules degenerate. In many mammals, long before birth, the entire *mesonephric* series loses its original urinary function and the original urine tube or *pronephric* duct also meets the same fate. The *mesonephric* tubules and duct persist in modified form as part of the reproductive system. The *mesonephros*, however, does not utilize the posterior part of the nephrogenic tissue, which forms a spherical mass in the roof of the lumbar region of the body cavity. A large number of kidney tubules appear in this mass, converting the whole mass into the *metanephros*.

The *metanephros* takes up excretory function in reptiles, birds and mammals as the *mesonephros* degenerates. It is not connected with the gonads. It develops quite late in ontogeny and shows no segmentation whatever. It is not possible to say as to how

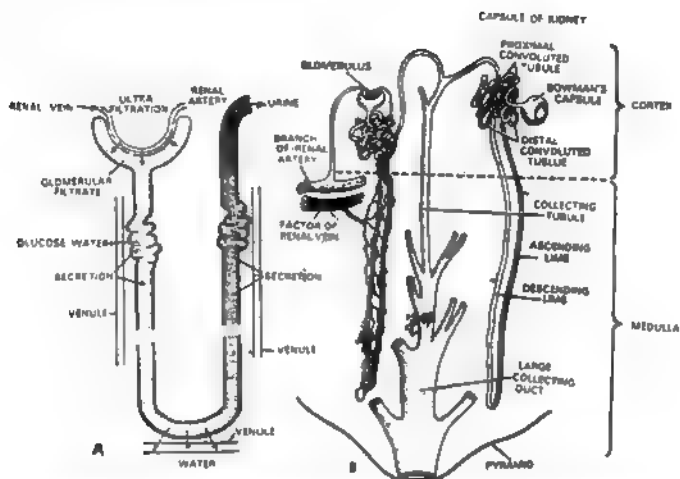


Fig. 8.63. A, Diagram of a generalised kidney tubule to show its mode of functioning. Differences in shading are an indication of changing concentration of the contained fluid; B, Uriniferous tubule and blood supply

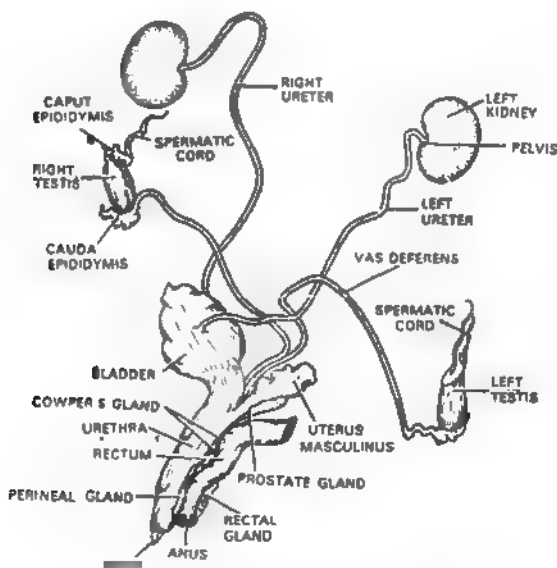


Fig. 8.64. Reproductive organs of a male rabbit

anterior end. It may be mentioned here that the collecting tubules, the pelvis and the ureter are outgrowths of the Wolffian duct.

Male Reproductive Organs. The testes are a pair of elongated ovoid bodies varying greatly in size at different times and about an inch and a half when fully developed. Each testis consists of a mass of coiled **seminiferous tubules**, bound by connective

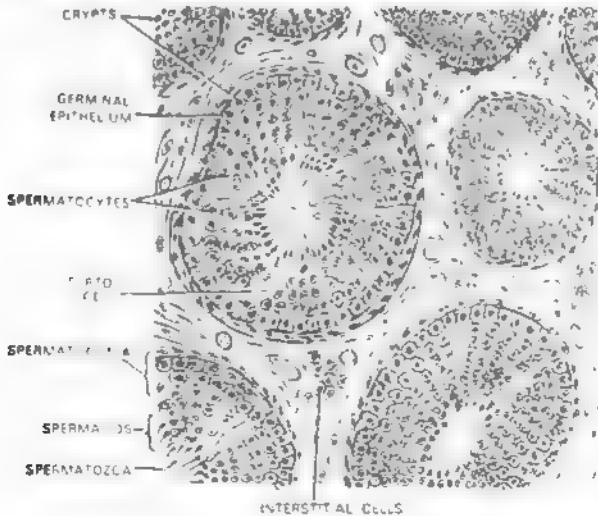


Fig. 8.65. Transverse section of the testis.

tissue, containing blood vessels and the **interstitial cells**. The latter produce hormones that influence the secondary sexual characters. Each seminiferous tubule is lined by **germinal epithelium** which gives rise to the spermatozoa. The interior of the tubules is occupied by the spermatozoa in the various stages of development (spermatogonia, primary and secondary spermatocytes, spermatids and spermatozoa). Certain larger cells (**Sertoli cells**) occur in between the germinal cells. These cells supply nourishment to the developing sperms (Fig. 8.65). A fibrous capsule, the **tunica albuginea**, surrounds each testis.

The testes are lodged in the scrotal sacs which are divided into two compartments by an internal partition. The cavity of the scrotal sac is in communication with the abdominal cavity through the **inguinal canal**. The external end of this canal is called the **external inguinal ring** and the internal end is the **internal inguinal ring**. In the early life the testes are abdominal in position lying against the dorsal wall of the abdomen close to the kidney. Before maturity they separate from the dorsal wall and descend into the scrotum through the inguinal canal. The testes are attached to the posterior end of the scrotal sacs but can be easily pulled back into the abdominal cavity. The ligament connecting the testis and scrotal sac is short but stout and is called **gubernaculum**. The duct of the testis is the **vas deferens** or **Wolffian duct**. It lies along the dorsal surface of the testis and is convoluted, the coiled portion being called the **epididymis**. The epididymis begins at the anterior end of the testis where it forms a cap-like structure of the coiled mass. This is called **head** of the epididymis or **caput epididymis**. It then passes down the dorsal surface of the testis as a coiled tube forming the **body** of the epididymis. At the posterior end of the testis it forms another coiled mass the **cauda epididymis** or **tail** of the epididymis. From this the vas deferens proceeds anteriorly, much convoluted tube and passes into the inguinal canal, where it

becomes a straight tube. Within the abdomen it loops round the ureter from the outer to the inner side and runs back to the neck of the bladder ultimately opening into the urethra. The posterior ends of the vasa deferentia are slightly dilated and run back side by side before opening. The head of the epididymis is derived from the mesonephros and is connected with the tubules of the testis by minute *vasa efferentia*. The remainder of the epididymis and the vas deferens are the Wolffian ducts. The spermatic arteries and vein enter and leave the epididymis at their anterior ends. Due to the descent of the testes these blood vessels elongate and run from their original abdominal places to the scrotal sac. They also carry nerve branches along with them. These structures together form the *spermatic cord*. At the place where the vasa deferentia and urethra join is located a blindly ending sac, the *uterus masculinus*. It is the sole remnant of the Müllerian ducts in male and opens by a crescentic opening in the dorsal wall of the urinogenital canal.

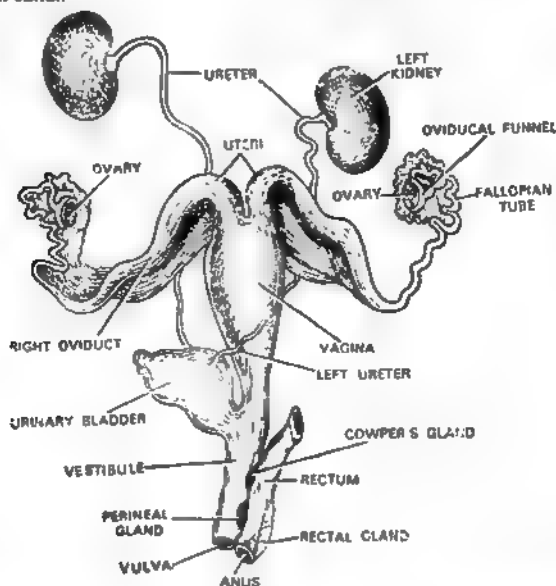


Fig. 8.66. Reproductive system of a female rabbit.

In the male the urethra is long and traverses an erectile intromittent organ, the *penis*. Ordinarily the urethra acts as a channel for conveying urine from the bladder to the exterior. During sexual activity the penis becomes erect and is introduced into the female reproductive tract to deposit the spermatozoa which pass through the urethra. The penis is an elongated body projecting from the ventral surface of the animal immediately behind the pelvic symphysis and in front of the anus. In the body of the penis the urethra is surrounded by three tracts of erectile tissue. These tracts include the posterior *corpus spongiosum*, through which passes the urethra and the anterior paired *corpora cavernosa*. Before copulation the blood rushes into these tracts, they become gorged with it and consequently the penis becomes erect. The free end of the penis (*glans penis*) is soft and obliquely truncated and is invested by a loose sheath of skin, the *prepuce*. In the flaccid condition the glans is retracted within the prepuce. The external opening of the urethra is situated at the tip of the penis and is a slit-like opening on its posterior face.

With the male reproductive system several glands are associated. Of these the **prostate** consists of a series of glandular masses grouped around the dorsal surface and sides of the uterus masculinus and vasa deferentia. They open into the urinogenital canal by slit-like openings of the short ducts. There are four or five lobes of the prostate. By far the largest is the **anterior lobe**, closely applied to the dorsal wall of the uterus masculinus and bilobed in front. Behind this is a smaller **posterior lobe** sometimes divided into two. A pair of still smaller **lateral lobes** lies in the angle between the vasa deferentia and the uterus masculinus. Behind the prostates lies a pair of **Cowper's glands** or **bulbourethral glands** of varying sizes. They are also placed on the dorsal wall of the urinogenital canal. Lying at the sides of the penis, and in the anterior walls of the perinaeal sacs are a pair of elongated, dark-coloured **perinaeal glands**, whose ducts open into the perinaeal sacs. Lying along the sides and posterior surface of the last two inches of the rectum are a pair of pale yellow **rectal glands**. They are much larger than the perinaeal glands.

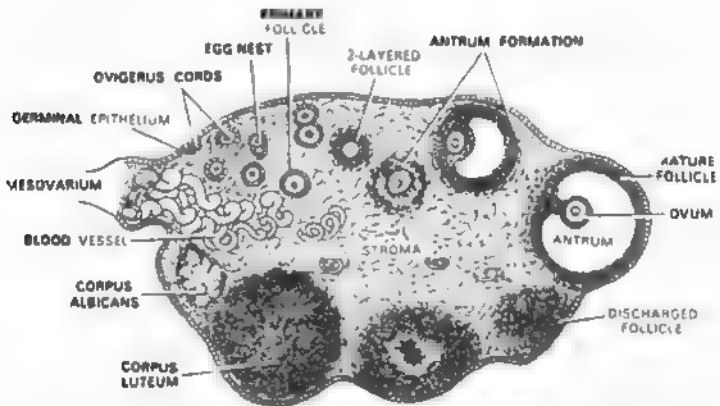


Fig. 8.67. Transverse section of the ovary (slightly diagrammatic) showing corpus haemorrhagicum (empty follicle soon after discharge of the egg), corpus luteum and corpus albicans, etc.

Female Reproductive Organs. As mentioned before the arrangement of the urinary system in the female is similar to that of the male except that in the female the urethra is a purely urine conducting tube, it has nothing to do with the reproductive system. The **ovaries** are a pair of ovoid bodies of pale yellowish colour and lie one on each side of the dorsal side of the abdomen. They are attached to the dorsal wall by a fold of peritoneum called **mesovarium**. The ovary of the mammal is a compact body, the bulk of which is made up of a mass of fibrous connective tissue and spindle-shaped cells, the two together forming the **stroma**. Egg-cells in different stages of development lie in the stroma. Each egg-cell is surrounded by a nourishing epithelial layer, the **follicle**. The follicle is made up of a row of single cells but with growth the rows of cell-layers increase. The **germinal epithelium** forms the outer coat of the ovary and it is this layer that gives rise to certain ingrowths into the stroma which form independent **primary follicles**. One of the group of cells enlarges to form the developing oocyte while the others form a single-layered follicle around it. As the follicle enlarges and sinks deeper and deeper into the stroma it requires a fluid-filled space, the **antrum**, the fluid being called the **liquor folliculi**. This crescentic space gradually becomes larger and separates the oocyte from the rest of the follicle cells except at one point, the **discus proligerus** (or **cumulus oophorus**) of which the innermost layer surrounding the ovum is called the **corona radiata**. The cumulus oophorus is continuous within the

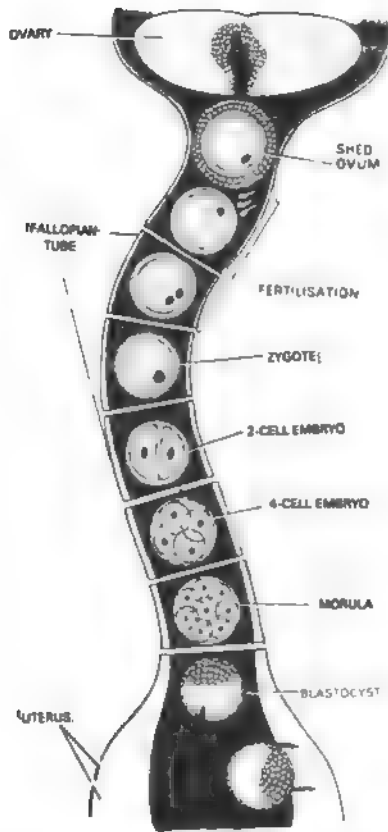


Fig. 8.69. Early stages of development of the rabbit including release of the egg, fertilization, cleavage, formation of blastocyst upto implantation.

smaller. The clitoris is erectile, but the urethra does not pass through it.¹

The Cowper's glands (bulbourethral glands) are reduced or absent in the female rabbit. The perineal glands and rectal glands are present in the female also and are similar in structure and disposition as in the male.

Egg. The egg is released by the rupture of the wall of the ovary. At the time of release it is in the form of a secondary oocyte. It is a small spherical cell (about 0.1 mm. in diameter in the rabbit) enclosed by a thin striated membrane called *zona pellucida* or *zona radiata*, secreted by the follicular cells. At the time of release the egg is surrounded by a number of large follicle cells called *corona radiata*. Soon after fertilization these cells disappear and in their place a dense coat of albumen is secreted by the walls of the oviduct. The amount of yolk in the mammalian egg is reduced very

¹ In the rat it is traversed by the urethra.

the organism. The surrounding cells constitute the **trophoblast**. The trophoblast cells which lie immediately above the inner cell mass are called the **cells of Rauber**. With further development the blastocoel increases so much so that the inner cell mass appears as a knob-like thickening at one pole, called the **embryonal knob**.

By this time the embryo becomes apposed and fixed to a small part of the uterine wall by means of the trophoblast. The joint reaction and development of the uterine mucosa and trophoblast is called **implantation** and leads to the development of the **placenta** through which the embryo exchanges nutrients and excretory products with its mother. This stage onwards the embryo remains attached to the uterine wall, from which place it does not move until it is born.

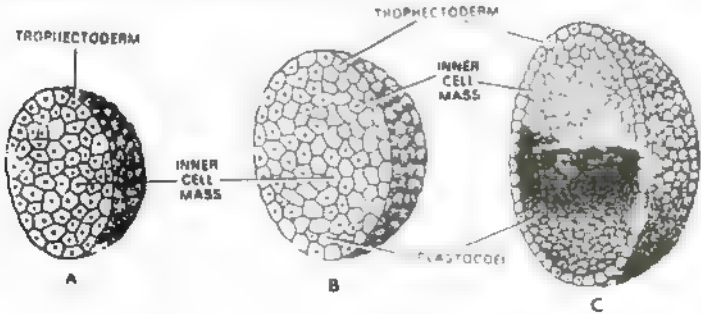


Fig. 8.71. Formation of the blastocoel. A, morula in section; B, blastocoel appears; C, blastocoel increases.

The development of a mammal takes place in two phases: the first begins with fertilisation and ends with the apposition of the blastocyst to the uterine wall and the second begins when the individual becomes intimately attached to its mother via the placenta and ends at birth. There is a very important difference between these two phases. The individual is small in the first or **free-living** phase and does not form specialised sets of cells, but from the beginning of the second or **fixed** phase, organ formation commences and this is accompanied by a rapid increase in the size of foetus. Throughout the free-living stage the embryo is sufficiently small and the uptake of nutrients and the elimination of waste product takes place from all its constituent cells by direct exchange with the local environment in this case the secretion of the Fallopian tube. In the second phase the foetus attains a great size, the cells are far removed from the surface as such exchange with the environment is not possible. Consequently the embryo develops a system primarily concerned with the exchange of nutrients and excretory products between all its cells and mother. This system comprises the foetal blood, heart and circulation. The mother's own capabilities become sufficiently great during pregnancy to deal with the extra-metabolic activity of the growing embryo.

Gastrulation. After the growth of the blastocyst for some time the inner (unattached) cells from side of the inner cell mass (roof of the blastocoel) begin to proliferate along the inner surface of the trophoblast to form the **yolk sac** (Fig. 8.72A). These cells have more darkly staining properties, and extend over the inner cell mass forming a layer called the **endoderm**. Its separation is the first step in the conversion of the blastocoel (excluding the embryonal knob) into the **yolk sac** which is not filled with yolk but merely with a fluid. Traces of disintegrating yolk cells cast out during cleavage may be seen in some cases (marsupials and certain types of eutherians but not in the rabbit). There is no doubt that at this stage the blastocyst represents the **gastrula** stage although the amniotic cavity has already made its appearance. The embryonal knob flattens soon after the separation of the endoderm layer and gradually increases in size. The cells of the embryonal knob become rearranged

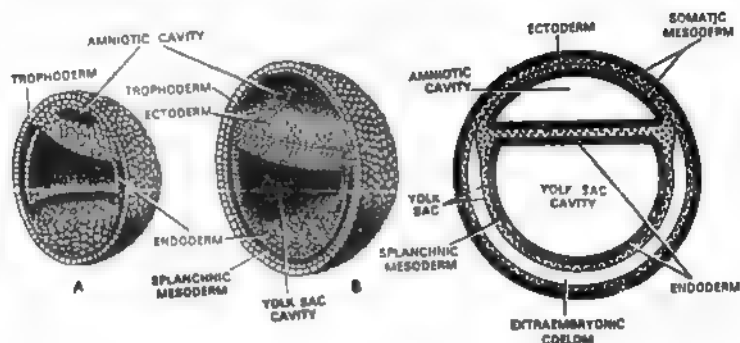


Fig. 8.72. Gastrulation of the mammalian embryo Amniotic cavity appears (A & B) and endoderm is formed.

forming a fairly regular epithelium. This is the area that can be compared with the blastodisc and it gives rise to the future embryo. It may now be called the **embryonal disc**. As the growth proceeds the cells (cells of Rauber) covering the embryonal disc, disintegrate and are then sloughed off or absorbed by the trophoblast, exposing the embryonal disc. By this time the zona pellucida of the original ovum and albuminous layers surrounding it also break and are absorbed.

The further development of the embryonal disc resembles, in broad outline, that of reptiles and birds. A **primitive streak** develops on the embryonal disc. It has all its components, viz., the primitive knot, primitive pit etc. It initiates the formative movements of cells, exactly as in the chick, ultimately separating the **mesoderm** and the **notochordal process**. For sometime, however, the notochordal process remains a hollow structure traversed by a **chorda canal** (also formed in reptiles). Formation of the **neural plate** follows the primitive streak. This finally develops the neural groove flanked by the neural folds which meet enclosing the neural tube, the forerunner of the

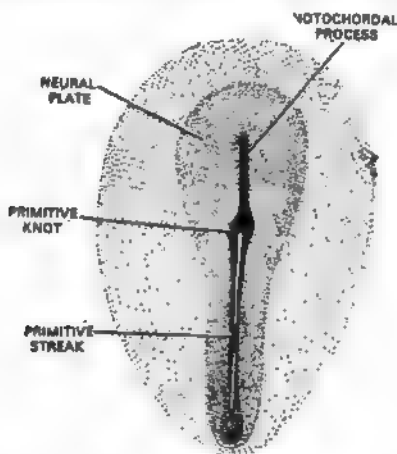


Fig. 8.73. Surface view of the embryo showing the primitive streak and neural plate.

mesoderm and the inner layer of trophoblast (ectoderm). The head and tail-folds advance towards each other ultimately fusing with each other. As the tail-fold is larger the **seroamniotic connection** lies above the anterior region of the embryo. With the fusion of these folds the embryo is enclosed by an ectoderm-lined amniotic cavity. Of the two layers formed as a result of this fusion the outer layer is the chorion and the inner layer is the **amnion**. After the fusion of the amniotic folds the trophoblast of the chorion develops villi, the **chorionic villi**, like those of the lower half of the blastocyst, which penetrate into the walls of the uterus.

Allantois. The endoderm beneath the hind end of the embryo grows out as a sac or vesicle and carries with it the overlying layer of splanchnic mesoderm. This vesicle is **allantois**. Its formation begins even before the amniotic cavity has become closed. In the chick embryo also it is formed in a similar manner. It enlarges rapidly and extends into the extra-embryonic coelom between the amnion and chorion. Evidently the allantois grows over the embryo outside the amnion. The allantois has a rich vascular

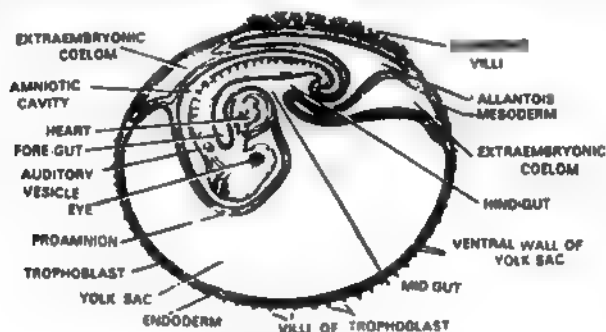


Fig. 8.77. Embryo showing the embryonic membranes.

supply right from the start. With further development some of these vessels become larger forming the **allantoic (umbilical) arteries and veins**. It has been pointed out above that the outer layer of the allantois consists of the splanchnic mesoderm. As the allantois enlarges this layer comes in contact with the mesodermal layers of both the amnion and chorion ultimately fusing with them. Thus the outer layer of the extra-embryonic wall becomes three-layered, outer trophoblast, middle double mesoderm (chorionic and allantoic) and endoderm. These layers are collectively known as **allanto-chorion**. The allanto-chorion plays important role in excretory and respiratory processes of the young animal as in the chick. But in the mammals it becomes more important because it also transfers nutritive material being a major part of the **placenta** (see below).

Yolk-sac. In mammals the original blastocoel becomes converted into the **yolk-sac** or **umbilical vesicle** (the name usually applied in mammals). The growing layer of endoderm lines the entire yolk-sac. The wall of the yolk-sac, at this stage, consists of endoderm and trophoblast. Soon the two layers of the extra-embryonic lateral plate mesoderm together with the extra-embryonic coelom extend downwards from the embryonic area between the endoderm and the trophoblast of the upper part of the yolk-sac. The splanchnic layer of the mesoderm comes in contact with the endoderm completing the wall (splanchnopleure) of yolk-sac, in which a vitelline circulation is established. The mesoderm does not penetrate the lower part of blastocyst which consists of only two layers, trophoblast and endoderm. The yolk-sac does not contain yolk as in reptiles and birds but it helps in conveying nourishment to the embryo. After some time the lower wall of the blastocyst ruptures so that the cavity of the yolk-sac communicates with that of the uterus. The uterine glands produce certain nutritive secretions, which fill the ruptured yolk-sac, from where they are absorbed into the

vitelline circulation. The yolk-sac helps the growing embryo to get its nourishment, but in a different way. The nutritive uterine secretions in some mammals (carnivores and ungulates) are produced in large quantity and are known as the *uterine milk*.

In most other mammals the embryonic membranes are formed in a different way. In the inner cell mass, a cavity appears which is destined to form the amniotic cavity. Because the amniotic cavity in the chick and others is ectodermal then this area must be ectodermal. This cavity increases and is separated from the yolk-sac cavity by a partition called the *embryonic disc* or *embryonic shield*, (Fig. 8.72 B). The disc develops into the embryo proper. Its dorsal layer (towards the amniotic cavity) is ectodermal, its ventral layer is endodermal and the cells between the two are mesodermal. Subsequently (or simultaneously) a large portion of the mesoderm is also formed between the yolk-sac and the trophoderm and between the ectodermal layer of the amnion and the trophoderm. From the very beginning the trophoderm is ectodermal (trophectoderm). It is now lined on the inside by mesoderm, and therefore corresponds to the serosa (chorion) of the chick embryo. The mesoderm between the yolk-sac and trophoderm now splits into two layers enclosing the third cavity of the embryo. The layer of mesoderm covering the yolk-sac from outside is the *splanchnic mesoderm*, that in the inside of the trophoderm is the *somatic mesoderm* and the third cavity is the *extra-embryonic coelom*, which in later stages is replaced by expanding amniotic cavity. In subsequent development the inner cell mass appears on the surface of the blastocyst and develops into the embryo proper.

Placenta In the evolution of reptiles to placental mammals the egg has lost its yolk and has returned to an isolecithal condition with less yolk than the egg of *Amphioxus*. This necessitates the early development of structures to draw nourishment for the embryo from the uterine tissues of the mother. To carry out such functions the embryonic membranes have become modified and have developed structures that enable the embryo to obtain nourishment from the uterus. For this the chorion and allantois have united to a greater or lesser extent in the different mammalian orders, and in conjunction with the uterine mucosa form the important embryonic organ called the *placenta*. It is an embryonic organ for the supply of oxygen and food and for the elimination of carbon dioxide and other wastes from the embryo. The placenta formed as a result of combination of chorion and allantois is called *allantoic placenta*, whereas in some mammals (marsupials) the placenta is developed by a combination of the chorion with the yolk-sac and is known as the *yolk-sac placenta*.

Yolk-sac Placenta. In *Didelphis virginiana*, the North and South American opossum (a marsupial) the blastocyst develops as described above. It develops an allantois and a large yolk-sac with a vascular network which is limited by a marginal blood vessel, the *sinus terminalis*. The yolk-sac is very large and makes contact with the chorion, which develops wrinkles and corrugations on its outer surface where it comes in contact with the uterine wall. These wrinkles tend to hold the blastocyst to the uterine wall, which secretes from its glands a nourishing viscid liquid which is absorbed by the blastocyst and transported by the vitelline circulation to the embryo. In the marsupial cat, *Dasyurus*, the chorion undergoes some more changes. It thickens by the formation of additional cells, which grow together forming branching syncytia. Now the uterine cells in contact with the chorion erode and the blastodermic vesicle sinks into it. The blastocyst in the opossum was held to the uterine wall by slight corrugations and here it sinks into a shallow depression. The yolk-sac is directed toward the uterine wall in the depression. This arrangement increases the chorionic surface to absorb the uterine milk secreted by the uterine mucosa (endometrium).

Allantoic Placenta In some marsupials such as the bandicoot (*Perameles*) the primitive allantoic placenta makes its appearance. In this case also a typical large yolk-sac develops supplied with a vascular system and a sinus terminalis. The allantois, here, also grows large and comes in contact with the chorion, which adheres to the uterine mucosa on that side where it is in contact with the allantois. At the place of contact, the blood vessels become concentrated in the uterine wall and the chorion of this region, more or less, degenerates. Thus, the allantoic blood vessels come in contact with the maternal blood. The primitive allantoic placenta, as such, is a flat and unfolded apposition of the allantois to the uterine wall. To facilitate the easy

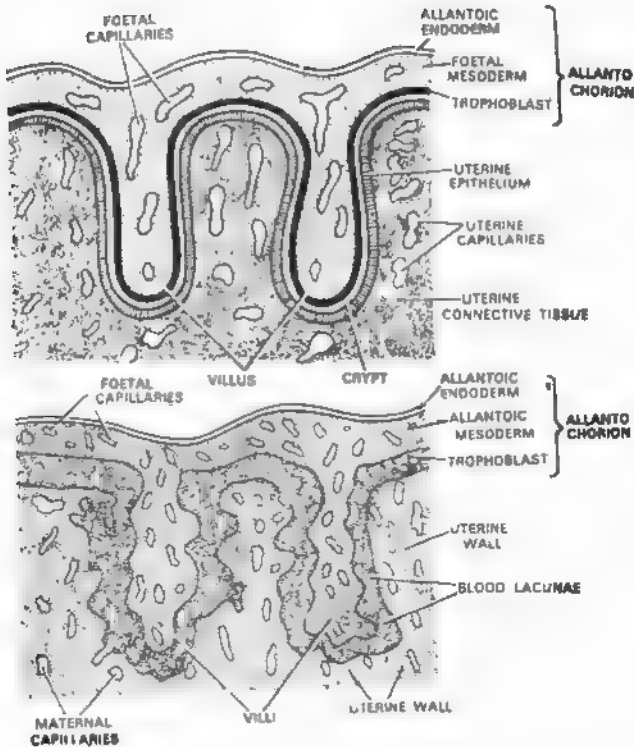


Fig. 8.79. Two types of placentas of mammals, A, epithelio-chorialis placenta; B, haemo-chorialis placenta.

In the **deciduate placenta** the union between the chorion and the uterine wall (endometrium) is much more intimate. The villi formed by the allanto-chorion penetrate the uterine mucosa and secrete certain enzymatic material that erodes the uterine tissue considerably establishing an intimate relation between the villi and the maternal tissue. The result of this intimacy is that at birth much of the superficial layer of the uterus called **decidua capsularis** is eliminated with the placenta, thus there is a definite loss of maternal tissue unlike that in the in deciduate variety. The deciduate placenta may be either of the **zonary** or **discoidal** type.

The **zonary deciduate placenta** is present in the carnivores. The blastocyst is elongate and is usually surrounded by two rows or zones of chorionic villi. The uterine wall is eroded. The villi branch profusely in the uterine tissue and each villus receives an extension of the allantois. The nutritive material derived from cellular breakdown or absorbed from the maternal blood is conducted into the embryo through allantoic circulation.

The **discoidal deciduate placenta** is formed in man. It begins its development on the entire surface of the blastocyst. In this case the blastodermic vesicle becomes embedded in the uterine tissue and is covered by it. Now as the blastodermic vesicle grows in size it projects into the uterus carrying a thin layer of uterine mucosa (**decidua capsularis**) over it. After some time the chorionic villi disappear on its free side and

increase on the sides attached to the uterine wall. The uterine mucosa, into which the latter is embedded, is called the *decidua basalis*. The syncytial trophoblast from the very beginning begins to erode the uterine wall. The result is that the uterine epithelium, uterine connective tissue and then the walls of the maternal blood capillaries disintegrate. The foetal connective tissue in the villi also disappears to a large extent. The maternal blood comes to circulate in lacunae in the thickened trophoblast of the villi. Thus the nutritive material diffuses through the trophoblast and the wall of the foetal capillaries only (as walls of the maternal blood capillaries are already lost).

It has been pointed out earlier that there is never any direct communication between the foetal and maternal blood streams. Several reasons have been put forward for this. Firstly the foetal blood vessels are delicate and would not be able to withstand the pressure of blood in the maternal arteries. Then in the maternal blood certain proteins specific to individuals are circulating. These, if transferred to the embryo, might prove harmful. The placenta, therefore, acts as a barrier and selects only such materials as suit the embryo. The blood also carries sex hormones that control the development of the secondary sexual characters, if the maternal blood stream were to become confluent with that of the embryo it is difficult to see how the secondary sexual characters of a male foetus and the mother could escape alteration.

There is another classification of the placentae that is based upon the relationship of the embryonic tissue (villi) and the maternal tissue (uterine wall). In the pig the villi penetrate the uterine walls but all the layers of the placenta are retained (indeciduate allanotic placenta). Such a placenta is called *epithelio-chorialis* type. In the cow and the sheep the uterine epithelium is eroded where the villi penetrate. Such a placenta is of *syndesmo-chorialis* type (cotyledonary indeciduate). In the carnivores there is a greater erosion of the maternal tissue, there is a breakdown of the uterine epithelium and uterine connective tissue, but the maternal capillaries remain intact (zonary deciduate). Such a placenta is of *endothelio-chorialis* type. All these placentae involve practically the entire surface of the trophoblast. Finally, there is the *haemo-chorialis* type of the placenta in which the uterine epithelium, the uterine connective tissue and even the walls of the maternal blood capillaries are eroded. The maternal blood comes to circulate in lacunae in the thickened trophoblast of the villi and the diffusion takes place through the trophoblast and the walls of the foetal capillaries. Such placentae occupy only a small area above the embryo (discoidal deciduate) and are found in man, rabbit, etc. In the rabbit, stages of foetal life, parts of the trophoblast finally breakdown so that the maternal blood bathes the foetal capillaries directly. The final rabbit placenta is therefore termed the *haemo-endothelial* placenta.

Parturition (Birth). The mother carries the developing young in the womb for a fixed period known as *gestation*. The period of gestation varies from a few weeks in smaller mammals to nearly two years in the elephant. Towards the end of this period the foetus starts looking like miniature adult. Then the wall of the uterus undergoes rhythmic contractions, the connection between the foetal and maternal layers in the placenta is broken and the foetus is gradually expelled through the vagina which becomes dilated for the purpose. Although the connection between the foetus and the placenta is cut off in the earlier stages of birth, yet a portion of the umbilical stalk remains attached to the foetus for a time. Finally, it shrivels and is absorbed, its position being indicated by the *umbilicus* or *navel*. Some time after the actual birth of the young animal, in most mammals, the foetal contribution, to the placenta and other foetal membranes are expelled. These are collectively referred to as "after birth".

GENERAL NOTES

Distribution. Mammals live on every continent, in mountains, deserts, arctic snows, marshes, meadows, forests, farms, cities and the depths of the sea. Some have become adapted to specific environments, thus, tree-squirrels live only in forests, rice-rats only in swamps. More adaptable mammals fit into a variety of environments thus, some rabbits live in woods, some in swamps, some in deserts. The walrus and some seals live in the Arctic seas and ice, other seals and sea-lions live along temperate ocean shores,

and whales and porpoises in the open sea. The beaver, muskrat, mink and others are inhabitants of fresh waters. Many rodents, carnivores and hoofed animals live in grasslands and forests, some mammals live in dense tropical jungles, while moles and pocket gophers live in the soil. The insect-eating bats are found hunting at night in the air.

Nests and Shelters. Most mammals need shelters for rest and sleep, to avoid inclement weather and to rear the young. Different mammals use different means to attain this. Some (wood-rats, conies and some carnivores) use natural crevices amid rocks, some (mice, raccoons, opossums, black-bears) use holes in trees and some bats resort to caves, trees or buildings. Some (tree-squirrels, some mice and some wood rats) build nests among the foliage of trees. There are many (rabbits, ground-squirrels, badgers, skunks), that dig burrows in the ground, and some of them (moles and pocket gophers) spend their lives in elaborate subterranean tunnels. Most elaborate constructions are those of the beavers that build mound-like houses of sticks and mud, construct dams and dig out canals. Many of the small rodents shred plant fibres longitudinally to form elongate shelters that are felted into warm soft nests.

Voice. Most of the mammals use their voices to express emotions and transfer ideas between individuals. The language consists of stereotyped calls, but is more varied among primates, leading towards the articulate speech of mankind. The call notes are used usually for the following purposes: (1) warning in time of danger; (2) to frighten and intimidate enemies, (3) to call the gregarious species to assemble; (4) to bring the sexes together for mating, and (5) to locate parents or young. In small bats short bursts of ultrasonic notes are produced, these echo from nearby objects and help to guide them in flight and in capturing prey.

Food. Mammals are herbivorous, carnivorous, omnivorous. Among the herbivorous mammals, there are two types, those that graze on grasses and herbs (horses, cattle, bison), and those that browse on leaves and twigs of shrubs and trees (deer, goats, elephants and giraffes). Rabbits eat grasses, herbs and bark and may forage on farm crops like other rodents. Squirrels and chipmunks eat different seeds, tree squirrels feed upon nuts, beavers eat inner bark of willow and aspen and porcupine eat that of conifers. The flesh eating or carnivorous mammals are many including the cats, weasels, mink, seals, whales and others. Wild cats often kill sheep or turkeys, foxes prey on poultry. There are many that subsist largely on insects (moles, shrews, skunks) but the small bats are exclusively insectivorous. Some mammals such as the house-rats and raccoons eat both plant and animal material and are called omnivorous.

The food requirements of small mammals are great. Some mice and rats consume nearly their own weight of food daily and a shrew has been reported to consume its own weight in insects during twenty-four hours. Seasonal scarcity of food that occurs is overcome in many ways. Some (squirrels, chipmunks, kangaroo-rat) collect seeds and store them by burying in the ground. The coney (*Ochotona*) also cuts and cures various plants as "hay" in summer and stores it in dry well-aired spaces among the rocks of its high mountain habitat. When the region is covered with ice this stored food is consumed. Some mammals solve the scarcity problem by migrating to areas with plenty of food. Such migrations are regular in many cases. The buffaloes of the great plains, for instance, migrate to northern grasslands for summer and retire to others further south for the winter. Some mammals (ground squirrels, chipmunk, bats) hibernate during winter to tide over food scarcity, some northern squirrels hibernating for about two-thirds of the year. The period of hibernation among the bears varies with altitude.

Enemies. Various carnivores depend on the herbivorous mammals for their food supply; cattle are eaten by tigers, antelopes and zebras by African lions. American deer by mountain lions, wolves and coyotes and so on. Weasels eat small mice. The mice, rats and rabbits are eaten by hawks and owls. Some large snakes are known to feed upon rodents. A major enemy of many mammals is man, who hunts game species, traps fur-bearers and kills the predators (or live stock) and crop feeders in various ways. Protozoans, flatworms, roundworms, lice, fleas and ticks are various parasites that attack mammals and reduce their vitality or destroy them.

Reproduction. Except in the lowest mammals (Monotremata) which lay reptile-like

Moles, voles and ground-squirrels help in making soil. Then there are many that damage the crops and domestic animals. Some harbour diseases that can be transferred to man. These diseases include plague, typhus and rat-bite fever in house rats; plague, relapsing fever and tularaemia in various wild rodents and trichinia in rats, pigs and cats. There are some large mammals (lions, tigers) that are directly dangerous to man.

The following mammals are notable among those that damage the crops of fields and gardens. Rabbits, woodchucks and some mice forage in vegetable patches, gardens and fields and may gnaw the bark of trees. Squirrels damage grain and other crops and many fruits. Bats damage guava groves and become a menace to keepers. The house rats gnaw into buildings, consume all kinds of foodstuffs and destroy much property. Since the beginning of agriculture, man has endeavoured to control the damage by rodents to his crops and property. The carnivores destroy large number of farm animals.

Conservation. The wild mammals are a natural resource, which should be used wisely for the long range benefit of all the people. Indiscriminate hunting, on the other hand, threatens many a valuable species to go into extinction. For this hunting and conservation laws have been framed which should be obeyed to get benefit. Threatened species such as bison, pronghorn and elk must be protected else they might disappear. Special National Forests have been created in many countries that are a reservoir of game and smaller animals. For the complete protection of wild life National Parks must be established. Even farms can maintain a mammal population. Hunting and trapping should be limited to removal of surplus animals only in order to assure a good supply in the future.

Fossil History. The mammals probably arose from the cynodont reptiles of Triassic time, that lived millions of years before the dinosaurs. The true mammals developed about 190 million years ago, but for over 100 million years they remained an unimportant group of animals, but in the Cenozoic era (Paleocene to Pleistocene) the mammals became dominant, as such the period is called the Age of Mammals. Within this period of about 55 million years many ancient mammals have disappeared leaving no descendants. Others that lived in those days gave rise to modern horses, camels, deer, beaver, bison and rhinos, to mention only a few. Small mammals were also abundant but their fossils are rare. Species that have become extinct recently include the following. The long horned-bison, one of a number of species of bison, widespread in North America during the ice age. Spear points found with bones of extinct bison show that man hunted them. The sabre-toothed cats, also found in Europe, were larger in North America. One species, with dagger-like teeth 8 inches long survived until late in the ice-age. The short-legged rhinoceros and kin developed in North America, became extinct before the ice age. Some migrated to Asia and Africa, where their descendants still live. American mastodon was of the early elephant-like animals that survived into the ice age as woolly mammoths and disappeared later. The giant ground sloth was an elephant-sized member of a group which today has few members. Heavy hind legs and tail suggest it squatted when feeding or resting. The early camel (*Procamelus*) represents the mid point in the development of the camel in North America. From here types of camels moved into Asia and South America where they live today.

Some early mammals were exceedingly abundant as is apparent from huge quantities of their teeth and skeleton dug out. Fossil relics of carnivores, whales, proboscidiens, horses, camels and others are sufficiently numerous so much so that the paleontologists have traced their probable evolution in detail.

CLASSIFICATION

The mammals are warm-blooded animals that suckle their young ones by means of mammary glands on females. The body is usually covered with hair (scant on some) which is moulted periodically. The skin is provided with glands, sebaceous, sweat, scent and mammary. Skull is provided with two occipital condyles, servical vertebrae usually seven and the tail is usually long and mobile. Two pairs of pentadactyle limbs

large coracoid; T-shaped interclavicle and precoracoids present; vertebrae without epiphyses; ribs with single capitulum, marsupial bones present; true teeth absent in the adult; ear without a pinna; male with a horny spur on the hind leg; right auriculo-ventricular valve incomplete; testes abdominal; ureters open into a urinogenital sinus which communicates with the alimentary canal, cloaca present, brain simple and without corpus callosum; eggs large and meroblastic and laid at an early stage; body temperature relatively low. But these animals are undoubtedly mammals because of the presence of hairs, warm blood, non-nucleated blood-corpuscles and a left aortic arch.

Order 1. Monotremata (Ornithodelphia). A very primitive subclass of Mammalia which lay eggs and possess many other reptilian features. They are regarded as mammals because they have hair and secrete milk. The fossil history of the group is unknown. The order is divided into two families, (1) Ornithorhynchidae, and (2) Echidnidae, which are closely related in many ways.

Tachyglossus (five-toed Echidna, family Echidnidae). The spiny-anteater is as large as the common cat. Skin is covered with spines and hairs; snout is elongated. Tongue is long and protractile. Tail is very short. Anterior abdominal vein is present. Each limb has five clawed digits. The area in which the ducts from milk glands open is depressed to form shallow pocket at the bottom of which open the milk-ducts. A few long hairs project from the pocket, possibly to guide the exuding milk into the mouth of the young whose beak is inserted into the pocket. A fold of skin in the vicinity of the mammary pockets forms a temporary marsupium in which the egg is incubated and the young retained for a time after hatching. *Echidna* avoids water and eats ants. Its strong claws are used for digging into ant hills and excavating deep burrows. Long sticky tongue is used for catching ants. Found in Australia, Tasmania and New Guinea.



Fig. 8.80. The five-toed Echidna.

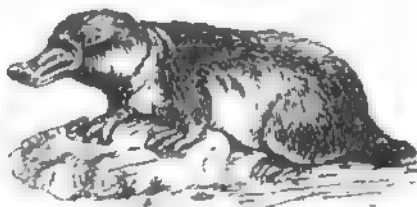
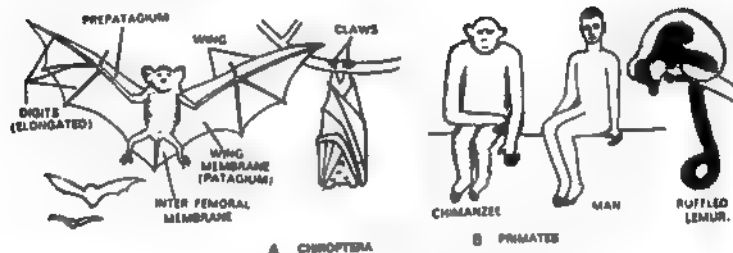


Fig. 8.81. The duck-billed Platypus

Ornithorhynchus (family Ornithorhynchidae). The duck-billed platypus is as large as a common cat. It has a stout body and a rather short dorsoventrally flattened tail. The head is small with laterally directed eyes. The snout is broad, elongated and covered with leathery skin produced into a fold at the base of the snout. The body is covered with a dense soft fur. The legs are very short, each with five digits, ending in strong claws. Webs of skin between digits are present (aquatic adaptation). About midway of the length of the body, ventrally, is a pair of slightly depressed spots of skin. On these spots open the ducts of tubular mammary glands. The young animal merely licks off milk as it exudes through the pores. It is semi-aquatic and burrows into the bank of stream or pond. The entrance to the burrow is under water, but the inner end, several yards in the interior is high and dry. It feeds upon small aquatic animals. Horny plates covering both the upper and lower jaws help to crush hard-shelled prey. It lays two eggs in a nest. Occurs in Australia and Tasmania.

SUBCLASS ALLOTHERIA

Order 1. Multituberculata. This order includes a series of small extinct mammals (**Plagiaulax*, **Microlestes*) chiefly known through the fossils of mandibles and teeth.

Fig. 8.34. A, The red-bat *Nycteris borealis*; B, Primates.

opposable pollex and hallux; low brain case, uncovered cerebellum. Orbit not completely shut off from temporal fossa, jugal posteriorly extended, nasals large; humerus with entepicondylar foramen, femur with third trochanter lower; incisors procumbent, lower canines incisiform, second toe and finger with a sharp claw; tympanic ring enclosed inside the bulla, uterus bicornuate. Madagascar, Africa and the Oriental region. *Lemur*, *Loris*, etc.

Sub-order Tarsioida. With large eyes and ears, long thin tail tufted at the end, very long tarsus, fingers and toes ending in flattened discs; inner upper incisor large and in contact with its fellow; molars with numerous pointed cusps, orbit largely separated from temporal fossa, digit two and three of the pes with claws; calcaneum and navicular elongated. Indo-Malaya Archipelago and Philippines. *Tarsius spectrum*.

Sub-order Anthropoidea. Monkeys, Apes, Man. Cranial cavity spacious and rounded orbits look forward and shut off from temporal fossa; dentition complete, with bunodont premolars and molars; two thoracic mammae; humerus without entepicondylar foramen, radius and ulna separate thumbs opposable; femur without third trochanter; opposable hallux; cerebrum covers cerebellum; uterus without cornua.

GROUP PLATYRRHINA

Superfamily Ceboidea. New-World Monkeys. With broad nasal septum; three premolars, tympanic-ring forms a bony canal to the external auditory meatus; tail may be prehensile.

The marmosets (family *Hapalidae*) are small, of the size of squirrels, head often provided with lateral tufts and tail is not prehensile.

The spider monkey (*Ateles*), capuchins (*Cebus*) and howlers (*Alouatta*) all present varied form and colour, though belong to the same family (*Cebidae*). The tail is prehensile in some. Some are very slender (spider monkey), some have loud voice (howlers), while others are mostly small.

GROUP CATARRHINA

Superfamily Cercopithecoidea. Old-World Monkeys and Apes. With narrow nasal septum; two premolars; bony external auditory meatus, ischial callosities, and cheek-pouches present; tail not prehensile.

Nasalis, proboscis monkey, occurs in Borneo; *Semnopithecus* (langur) occurs in India, and includes the sacred God Hanuman; *Colobus* occurs in Africa with hair long, black-and-white; *Cynocephalus* (baboons) with stout head, dog-like, tail short with savage disposition; *Macacus* (macaques or rhesus monkeys) mostly occurs in Asia (one species is reported from Gibraltar). It is used as pet and also in biological research.

Superfamily Homonoidea. Anthropoid apes and Man. Tail and cheek pouches are absent.

Anthropoid apes (family **Pongidae**) include the following; *Hylobatis* (gibbon) and *Siamanga* (siamang) are chiefly arboreal travelling easily through the trees; the body is slender; limbs long; height about three feet, walk slowly on the ground using only feet; these omnivorous anthropoids have powerful voice, often used. They occur in southeastern Asia and Malaya Archipelago. *Pongo* (Simia), *Satyrus* (orang-utan) has a flattish face, high-topped skull and man-like brain. It is about 54 inches tall, has long hair, lax and reddish. Old males often with beard. Lives in trees and prepares crude nest, feeds on plant materials. Occurs in swamps, forests of Sumatra and Borneo. *Gorilla gorilla* has heavy body and limbs. The male is about 65 inches high and 500 pounds in weight; hair and skull are black; walks on soles of feet aided by knuckles of hands, with body inclined, lives chiefly on ground in family groups. Feeds on plant materials. Occurs in West and East Central Africa. *Pan* (*Anthropopithecus*) *troglodytes* (chimpanzee) is also large (54 inches high and 150 pounds heavy) with round head, large ears and short fore-arms. It resembles man more than any other anthropoid; feeds on plant material. Occurs in the forests of West Africa.

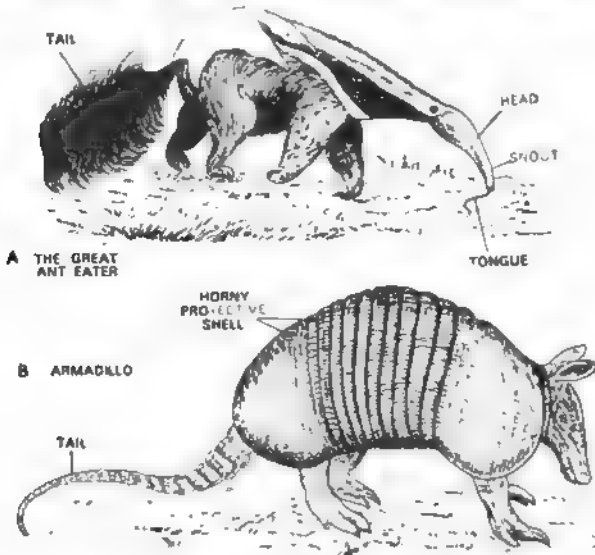


Fig. 8.85. The Edentates. A, great ant-eater or *Myrmecophaga jubata*; B, an armadillo, *Tatusia*.

Man, *Homo sapiens*, belongs to family **Hominidae**.

*Order 5 **Tillodontia**. Paleocene-Eocene.

*Order 6 **Taeniodonta**. Eocene.

Order 7 Edentata (Xenarthra). Teeth absent from the anterior part of the mouth; with scratching or curved claws on the extremities; with numerous rootless grinders. Eocene to Recent. Includes ant-eaters, sloths and armadillos. The ant-eaters include *Myrmecophagus* (family **Myrmecophagidae**) with elongate head and snout, slender, protrusible, sticky tongue, fore feet with stout curved claws used to open ant and termite nests. Body covered with long hair. There are two other genera *Tamandua* with less long snout and *Cyclopes* the small tree living ant-eater.

The sloths (family **Bradypodidae**) are very fully adapted for arboreal life. The face is short, head large and the body is covered with long hair. Molar teeth are present. All feet are long, especially the fore-limbs, and the digits carry hooked claws for hanging

Sloths hang upside-down on tree branches. Eat fruits, leaves and birds. Occur in tropical America. Examples include *Bradypus* (3-toed sloth) and *Cholocepus* (2-toed sloth).

The armadilloes (*Dasypodidae*) are a very ancient group already differentiated in Paleocene times. Bony plates develop in the skin and are covered by horny scutes forming a horny protective shell which is commonly divided by transverse furrows of softer skin so that the animal can curl up when disturbed. *Dasypus*, the nine-banded armadillo, is a common form about 16 inches long found as far north as Texas.

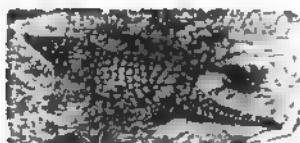


Fig. 8.86. The Pangolin, *Manis* sp.



Fig. 8.87. *Manis* rolled up as a protective measure.

Order 8. Pholidota. Pangolins. The scaly ant-eaters of the Old World (Africa and Asia) are covered with overlapping epidermal scales which can be erected, and with hairs between the scales. Teeth are absent and the tongue is long and extensible. The limbs are short and carry five digits. They walk on the dorsal surfaces of the claws of their fore-feet and on the soles of the pes. Terrestrial and burrowing forms that can roll themselves into a ball as a measure of protection (Fig. 8.87). Some are able to climb trees. All are nocturnal and eat ants and termites. *Manis* has many species, some live in tree-less plains or meadows and other can climb trees.

Order 9. Lagomorpha. The rabbits and hares are nowadays considered to be a very isolated off-shoot of the early eutherian stock, whose similarities to the Rodentia may be only superficial. The lagomorphs are small to moderate in size with small stubby tails. Toes are provided with claws. Chisel-like incisors grow continually; upper incisors two pairs, canines are absent, molars unrooted, palate broad jaw motion only lateral; elbow joint non-rotating. Eat leaves, stems and barks. Eocene to Recent. More than 200 species and subspecies are found. Include pikas or conies, hares and rabbits.

Pikas or Conies (not Hyracoidea) belong to family *Ochotonidae*. *Ochotona* occurs in California and Colorado to Alaska and Asia, at high altitudes. About six inches long it has rounded ears, equal legs and vestigial tail. They live about rock piles and gather plants for "winter hay".

Hares and rabbits (family *Leporidae*) possess long ears, long hind-limbs for jumping. Feed on leaves and stems of plants. *Lepus americanus*, snow-shoe hare, turns white in winter; and *L. campestris*, or "jack rabbit", both are surface dwellers and young are hairy when born. *Lepus (Oryctolagus) cuniculus*, the European gray rabbit, source of all domestic breeds, introduced and widespread in Australia and New Zealand.

Order 10. Rodentia. The characteristic features of the rodents are the incisors, one pair only of which persists in each jaw. The incisor has enamel on its interior surface and thus maintains a cutting edge; canines absent; with wide diastema between incisors and cheek teeth. They are small herbivorous, plantigrade, unguiculate; articular surface of the lower jaw longitudinally elongated; palate narrow; jaw



Fig. 8.28. The Rodents. A, The porcupine *Kerthirossen darwini*; B, the gray squirrel, *Sciurus carolinensis*; C, the grasshopper mouse, *Onychomys leucogaster*.

muscles much enlarged; jaw movement both fore-end-aft; clavicles absent; elbow joint rotates; brain shows little convolutions; caecum large; body covered with fine fur which may be modified into spines, nails usually claw-like, the habit of gnawing food is universal. Occur from Eocene to Recent. The rodents are world-wide in distribution, found in many continents and many islands, from sea level to above 19,000 feet in Himalayas, from dry deserts to rain forests, some occur in swamps and some in fresh water but none in the sea. Majority of living mammals belong to this order. More than 6,400 species and sub-species are known. Size varies from 2 inches long mice to 48 inches long capybara (*Hydrochoerus* of South America) although the average size is below 12 inches. Some are partly or largely insect-eating forms others eat leaves, stems, seeds or roots. Smaller species have a high reproductive potential. Are eaten by many carnivorous mammals, birds and reptiles. Squirrels, pocket gophers, pouched mice, rats and mice, porcupines and beavers are examples of this order.

The squirrels (family *Sciuridae*) are most diurnal and feed chiefly on seeds and nuts. The ground as well as tree species and some species such as woodchucks which do not look like squirrels at all belong to this. All squirrels have bushy or furry tails and fairly rounded heads, *Sciurus*, tree-squirrels (red, gray, fox, etc.) occurs in forest regions. *Citellus*, the ground-squirrels on open lands. *Marmota*, commonly called woodchuck, ground hog or marmot live in meadowlands, feed on grasses. *Glaucomys*, the flying-squirrels, with broad membranes along the sides of the body, live in forests and are nocturnal in habit.

The pocket gophers (family *Geomyidae*) are burrowing rodents with short naked tails and fur lined cheek pouches for carrying food. With their powerful clawed front legs they dig tunnels, which they seldom or never leave. Food is roots and stems. There are three major genera and about 260 species *Geomys*, *Thomomys*.

The pouched mice (family *Heteromyidae*) with fur-lined cheek pouches, forage on surface of ground at night, chiefly seed eaters. *Dipodomys*, the kangaroo mice are good jumpers, *Perognathus*, the pocket mouse are small ($3\frac{1}{2}$ to 6 inches) with small ear and tails.

The rats and mice (family *Muridae*) are of different types *Microtus*, meadow mice or voles are the most common and most prolific of the rodents. One female in captivity had 17 litters a year. *Peromyscus*, white-footed or deer-mouse are widespread over North America. *Sigmodon*, cotton rats, *Neotoma*, wood-rats, and *Ondatra*, muskrats, are others. The muskrat is valued for fur. *Rattus norvegicus*, Norway rat, *R. rattus* black and roof rats; *Mus musculus*, the house mouse are the common rats. The old world rats and the house mouse has been spread by commerce and shipping to all civilized countries. They damage property and food supplies and spread various diseases including plague, typhus and ratbite fever.



Fig. 8.89. The common drain mouse *Rattus norvegicus*.

The porcupines (family *Erethizontidae*) are large (length up to 30 inches; weight up to 40 pounds) clumsy rodents covered by spines especially on the back and tail. These spines are loosely attached and barbed and can seriously injure or kill an attacking animal. These spines are not quills but modified hairs. They feed on wood and inner bark (cambium) of many trees. *Erethizon* and *Hystrix* are the common genera with several species.

The beavers (family *Castoridae*) occur in North America and Europe and were common formerly. Head and body length about 10 inches; tail flat oval scaly; body pelage soft with a desirable fur. Build dams on streams with sticks and mud to form ponds around their big one-room houses with under water entrances. At night they gnaw down trees and float branches through canals to the ponds. Eat fresh inner bark of trees and store branches under water for winter food. They mate for life. The young (two to six) are born in spring. Beaver skin is valuable, dams are important for flood control.

Order 11. Cetacea. Whales and Dolphins. Body fish-like and stream-lined, naked, but with a thick layer of sub-cutaneous blubber; nasal apertures on the top of the head, caudal fin horizontally expanded, fatty dorsal fin present, external ear minute and devoid of a pinna, eyes very small and at the angle of the mouth. Live in "schools" (herds) and swim with great strength and speed; carnivorous and predaceous; found in

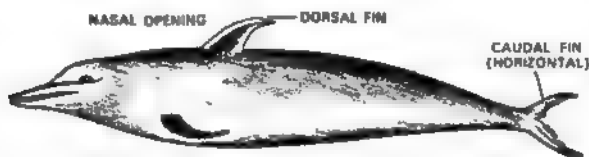


Fig. 8.90. The Cetacean, dolphin

all seas. Whale and their kin form large group found in all open seas and along many shores, a few even live in rivers and fresh water lakes. These range from small 5 feet dolphins to great Bhu whales which have occasionally reached 100 feet in length and 150 tons in weight. These are the largest animals that have ever lived. They are larger than the dinosaurs and weigh as much as twenty to thirty elephants. They are descendants of land animals and breathe air for which they come to the surface.

The whales are divided into two distinct groups, the Mysticeti or Baleen (whalebone) or toothless whales and the Odontoceti or toothed whales including dolphins and porpoises.

*Sub-order *Archeoceti*: Zeuglodonts. Eocene to Oligocene.

Sub-order *Mysticeti*. Oligocene-Recent. Whalebone whales without teeth.

Balaena, "right" whale, Arctic.

Sub-order **Odontoceti** Eocene-Recent Toothed whales. With numerous small homodont and monophyodont teeth.

Platanista gangetica, the Ganges dolphin.

Order 12. Carnivora. The carnivores are well-known mammals, quick, intelligent and sometimes vicious. Many of them are built for speed the notable being the cat family. Most carnivores are predators and show adaptations for hunting. The most obvious are in the mouth, the lower jaw moves freely for grasping and gripping, teeth are sharp for cutting and tearing. The feet of carnivores are padded, some with sharp claws. Of the several families of carnivores two (the seals and walruses) are aquatic. Though the rest are land animals some species (river- and sea-otters) are excellent swimmers, adapted to water life. The carnivores range in size from the tiny least weasel to half-ton bears. Some supplement their diet with fish; a few eat fruits and berries. The group includes some of the best fur-bearers (otter, mink, marten, fox and raccoon) some of which are raised on fur farms. The carnivores keep the rodent-population in check.

*Sub-order 1. **Creodonta.** Eocene to Miocene

Sub-order 2. **Fissipedia.** Dogs, cats, bears, etc. Terrestrial-Carnivora with large projecting canines, three incisors; cutting pre-molars, molar tuberculate, carnassial teeth present; clavicles absent or reduced, scaphoid, and lunar fused in the carpus, limbs ungulate and provided with strong claws; orbits are not closed behind, sagittal crest formed at the union of parietals; tympanic forms a bulla; zygomatic arch is strong and stands well out from the cranium to allow for the powerful jaw muscles. Most of them flesh eaters, but some eat plant materials. Pelts of many form valuable furs.

Members of the dog family (family **Canidae**) are familiar widespread carnivores found the world over. Most of them are medium-sized, active, gregarious animals best described as "dog-like". Different species are similar markedly through the ages. Fossils of 30 million-years old "dogs" indicate that they were much like those of today. Examples include *Canis lupus* (wolf); *C. latrans* (coyote or "prairie wolf") under 30 pounds in weight, eat rodents, deer, antelope, domestic sheep and plant material; *Canis domesticus* dog; *Urocyon*, gray fox in brushlands; *Vulpes*, red fox chiefly occurs in woodlands, now it has been domesticated and "black" and "silver" phases are reared on fox farms.

The raccoon (family **Procyonidae**) identified by black mask and ringed tail, feeds on rodents, insects, frogs and corn and washes its food when near water. They are about 30 inches long, curious, mischievous but make fair pets. Pelts used for coats. *Procyon lotor* is the raccoon found in most of United States. *Ailurus*, panda, occurs in Himalayas; *Ailuropoda*, giant panda occurs in mountains of Western China, feeds on bamboo.

The bears (family **Ursidae**) are of many types. The black bears *Euarctos americanus* is a large species six feet long weighing up to 600 pounds. It climbs trees readily and hibernates in midwinter. They also have a brown phase. *Ursus arctos horribilis*, the grizzly bear, is the largest of land carnivores. Once widespread and freely hunted it is today protected in most regions. *Thalarcos maritimus* is the polar bear of Arctic regions, pelage white and dense, feet fully furred, teeth pointed, food of fishes and seals.

The cat family (family **Felidae**) includes large and small species but all have a few common characteristics, short faces, blackened rough tongue, sharp cutting teeth and padded feet with retracting claws. Formerly this family was widely distributed, but now all species and especially the larger cats are reduced in number and in range. The common domestic cat *Felis catus* is a descendant of a Libyan cat tamed by Egyptians centuries ago. Like its wilder relatives it feeds on rodents, other small mammals and birds. Other cats include *Felis leo*, the African lion, *Felis tigris* the tiger found in eastern Asia and India, both large and dangerous to man. *F. cougar*, the mountain lion (cougars, pumas or panthers) feed on deer, sometimes colts and live-stock about 8 feet long and 200 pounds in weight, now very rare, leaps on prey from trees or rocky ledges, fears and avoids man. *Lynx* is a handsome, sub-tailed about 3 feet long cat with thick soft fur; *L. rufus* is the wild cat or bobcat which is a fearless hunter that may attack

The eared seals (family *Otariidae*) include *Eumetopias jubata*, Steller sea-lion occurs from California to Alaska, *Callorhinus ursinus*, northern fur seal, (were once nearly exterminated, now number nearly 4 million with a potential fur value of 100,000,000 dollars); and *Zalophus californianus* smaller Californian sea lion (8 ft. long 600 pounds in weight). All circus seals are Californian sea lions.

The walrus (family *Odobenidae*) have thick skin, sparsely haired, two upper canine teeth form tusks up to 3 feet long used to dig crustaceans and molluscs on sea bottom. These teeth are used by man as ivory. *Odobenus*, in Arctic is about 10 feet long.

The earless or hair seals (family *Phocidae*) are less agile on land because their hind-legs cannot be turned forwards. *Phoca vitulina*, harbour seals, are common on coasts and bays; *Mirounga*, sea-elephant is about 18 feet long, occasional inhabitant of southern California.

*Order 13. *Condylarthra*. Paleocene to Eocene.

*Order 14. *Litopterna*. Paleocene to Pleistocene.

*Order 15. *Notungulata*. Paleocene to Pleistocene.

*Order 16. *Astrapotheria*. Paleocene to Miocene.

Order 17. *Tubulidentata*. Aardvarks. These are very isolated forms with unknown affinities. The body is like a small pig with a highly curved back, ears and snout long, mouth tubular with slender protrusible tongue, as in other anteaters. The peg-like teeth with tubes in the dentine are unlike those of any other mammal. Milk teeth numerous, permanent teeth fewer (no incisors or canines) unrooted, no enamel. Toes, 4, 5, with heavy claws for digging. *Orycteropus*, the cape ant-eater or 'earth pig' has two or three species, nocturnal in habit, digs out nests of ants and termites on which it feeds.

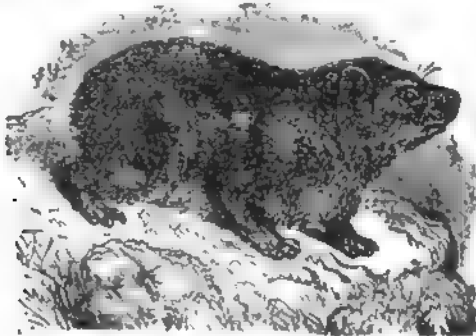


Fig. 2.92. The Hyracoidea, Hyrax.

*Order 18. *Pantodonia* (*Ambylopoda*). Paleocene to Eocene.

*Order 19. *Dinocerata*. Paleocene to Eocene.

*Order 20. *Pyrotheria*. Paleocene to Oligocene.

Order 21. *Hyracoidea*. The Biblical conies. Small rabbit-like creatures with close set fur, small ears and a split snout, tail reduced. Most of these live on the ground except *Dendrohyrax* which lives in trees. The animals are herbivorous. Inhabit Africa. Oligocene to Recent. One genus *Hyrax* (*Procavia*) with about 14 species superficially like guinea pigs but related to hoofed animals.

Order 22. *Proboscidea*. The Elephants. Large animals with enormous head; with a long, mobile proboscis serving as a prehensile organ, nostrils at the end of the proboscis; limbs massive pillar-like semiplantigrade; incisors of great size and form tusks canines and premolars absent; molars lophodont. Gregarious, live in herds of 10 to 100, feed on trees grass and bamboos. Love dark and shady forests; herbivorous.

9. THE ENDOCRINE GLANDS

There are two types of glands in the body, those that discharge their secretion through ducts on the surface of the body and those that do not possess ducts and pour their secretion directly into blood stream. The former are known as the glands of external secretion or **exocrine glands**, the latter are the glands of internal secretion or **endocrine glands**. The secretions of the endocrine glands are very important products of the body and are responsible for co-ordination within the body. For the most part they are excitatory in their actions. They stimulate the growth and development of the functional activity of certain tissue. These internal secretions are called **hormones** (Gr. hormao, I excite) or **autocoids**. The hormones are catalytic in action and act in very small quantities. Although they hasten chemical actions but themselves they do not change permanently. Certain glands with ducts (pancreas, gonads, etc.) also produce hormones in addition to other substances they deliver through ducts. The term hormone denotes any substance formed by a tissue and carried in the blood stream to act as an excitant to some other tissues or organs. Thus carbon dioxide, which acts upon respiratory and vasomotor centres, and secretin which causes secretion of the pancreatic juice come into this category. Some ductless glands produce chemicals which control (inhibit) rather than stimulate the activities and are called **chalones**.

The hormones are released directly in the blood and carried everywhere by the blood stream but they act only on certain specific organs. That is to say that the endocrine glands are interdependent. Disorders in the balance of endocrine activities produce several pathological conditions. Hormones also control emotional activities of the animal, loss of the glands of internal secretions may prove fatal.

The endocrine system in an animal controls the following activities : (i) the time, order and rate of organic development, (ii) metamorphosis in amphibians, (iii) adaptive coloration of certain larval salamanders, (iv) development of secondary sexual characters, and (v) many phases of behaviour, especially emotions that

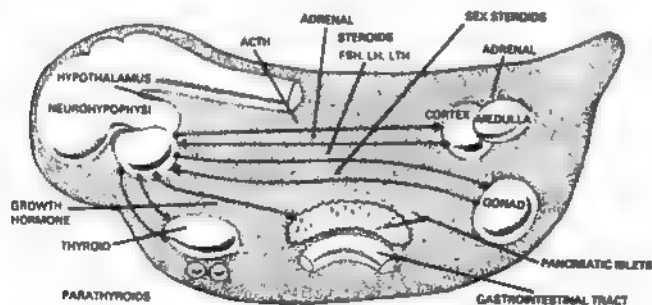


Fig. 9.1. The Vertebrate Endocrine glands and their inter-relationship.

contribute a lot to the psychic life and to the determination of personality. Most of the endocrine glands are present in all orders of vertebrates and an extract obtained from the gland of one order exerts its specific effect when administered to a member of another order. For instance, the extract of sheep's thyroid influences the growth and development of the tadpole of the frog.

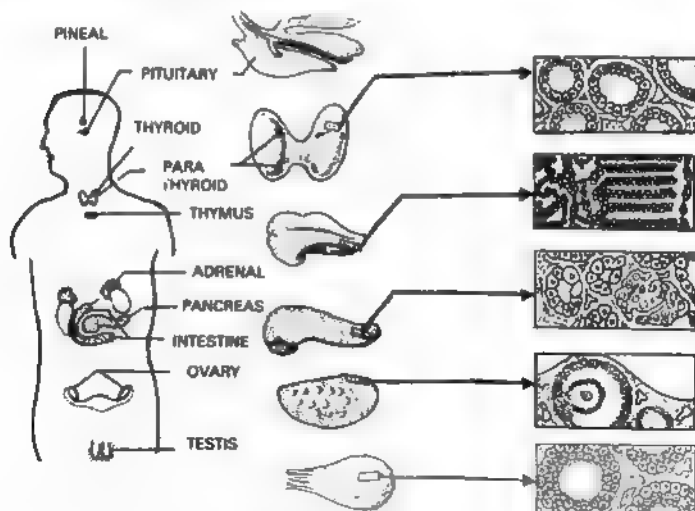


Fig. 9.2. Sites, shapes and structure of different endocrines in man.

The endocrine glands have been grouped according to location for the sake of convenience in study. The glands lying in the neighbourhood of the pharynx are called the (i) **pharyngeal endocrine glands** and include the thyroid, the parathyroid and associated glands. (ii) The **cranial endocrine glands** such as the pineal and the pituitary lie in the head. (iii) The **abdominal endocrine glands** include the pancreas, intestinal glands and the adrenals all lying in the abdomen. The **sexual endocrine glands** are also located in the abdomen but they may be separated because they differ from the rest in being glands with ducts that pour hormones directly in the blood stream.

Thyroid Gland. The thyroid (Fig. 9.3) is one of the oldest structures of the pharyngeal region. It is believed to have originated from the **endostyle**, an open, ciliated, mucous producing groove of tunicates and **Amphioxus**. In higher vertebrates it originates as an evagination from the same region (between first pair of gill pouches) of the pharynx with which it remains connected only for a short time. Soon it becomes disconnected and takes the form of a ductless gland. In the ammocoete larva of the lamprey eel, however, the duct remains functional.

The basic histologic unit of all vertebrate thyroid glands is the **follicle**, a hollow ball consisting of a single layer of epithelial cells enclosing a fluid-filled space (Fig. 9.2). The epithelium is capable of extreme variation in shape within the same species or within the same thyroid gland in different physiologic states. Tall columnar cells are found in very active gland, while low squamous cells are associated with reduced function.



Fig. 9.3. Outlines of the shapes of thyroid glands in different groups of vertebrates.

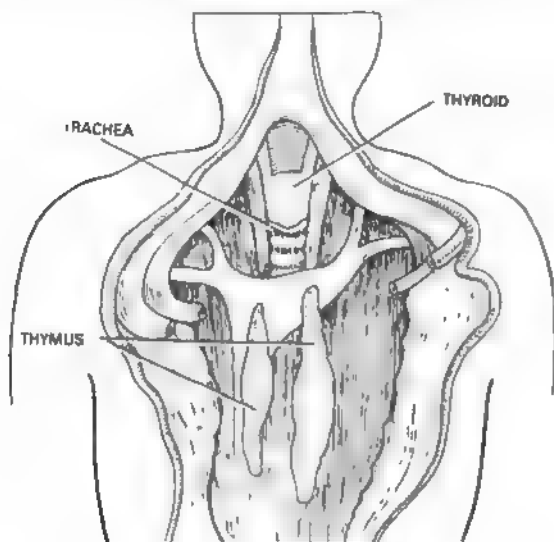


Fig. 9.4. Thyroid and thymus in one month old child.

The alveolar cavities are filled with a homogeneous gelatinous material (colloid) secreted by the lining cells containing the thyroid hormone. The colloid is the site of storage of a protein-bound form of the thyroid hormone, so that the gland is also unique in having the only extracellular storage of hormone within the gland. The colloid may also show some changes associated with different stages of function.

With the help of electron microscopy additional information has been made available recently. Apart from usual features (endoplasmic reticulum and mitochondria) the thyroidal cytoplasm contains a larger than usual variety of granules of different sizes and densities. The nature of some of these granules is still unidentified.

The special function of the thyroid glands is the accumulation of iodine and its union with throsine to form thyroid hormone (thyroxine) which is formed in several phases under the control of the thyrotropic hormone of the pituitary (TSH). The entire mass of follicles or alveoli is surrounded by connective tissue. The gland has a generous blood supply being connected with both the carotid and subclavian arteries. According to Wiedersheim the blood supply of the thyroid is richer than that of the brain. The active mammalian thyroid gland is said to carry a larger flow of blood per unit of tissue weight than any other organ. The thyroid is supplied with nerves, but whether these control the secretory activities is questionable.

In the lower vertebrates such as fishes the thyroid is represented by groups of loose follicles scattered along the ventral aorta. In the amphibians, reptiles and birds it becomes more and more compact. In elasmobranchs it is an unpaired structure lying just in front of the division of the ventral aorta into two. In teleosts it is paired. In amphibians it is paired lying in the region of the hyoid apparatus. Among reptiles it is unpaired in Ophidia, Crocodilia and Chelonia and lies close to the anterior surface of the pericardium on the ventral aspect of trachea. In lizards, on the other hand, it lies transversely stretched on the ventral surface of the trachea and consists of a large median portion and a pair of comparatively small lateral parts. In birds the thyroid is paired consisting of two separate bodies, a right and a left, lying at the base of the neck, the right being slightly anterior to the left.

In mammals the thyroid is a compact bilobed structure, the two lateral lobes are connected by a strand of tissue (isthmus). It lies on the ventral side of the posterior end of larynx. In some carnivores (cats or lion) the isthmus is wanting. In some, when it is present, it consists only of connective tissue fibres. In man and other primates the isthmus is made up of parenchymatous cells. In man the two lobes lie on either side of the larynx and in the adult it weighs about 40 grams.

Functions. The thyroid gland may be defined in a very simple way as the tissue which is capable of accumulating iodine in great excess and combining it into an organic compound thyroxine. In recent years a tremendous surge of thyroidal research has been made possible by the fortunate availability of radioactive iodine. The thyroid hormone and its precursors are the only iodine compounds in living organisms. Thyroxine has been chemically isolated and crystallized and has also been artificially synthesized. The principal function of thyroxine is to maintain the metabolic process of the body at a sufficiently high level.

The list of organs, organ systems and metabolic processes affected by thyroid hormone is by far longer than that of any other hormone. It is believed to influence such diverse activities as (a) guanin deposition in the fish scale, (b) melanin deposition in birds feathers, (c) threshold stimulus sensitivity in nervous receptors, (d) closure of epiphyses in bones, (e) schooling behaviour in fishes, (f) creatine creatinine conversion, (g) exchange of water and salts between cell body and fluids, and (h) water diuresis (discharge of excess urine).

Various morphologic effects of thyroid hormone are shown during metamorphosis of frog. When fed on thyroxine the tadpoles quickly lose their horny teeth (used for eating plant material), grow hind limbs and fore limbs, shorten their intestines in anticipation of carnivorous feeding, resorb their swimming tails, modify their skin structure for terrestrial life, and emerge from aquatic to terrestrial environment. If

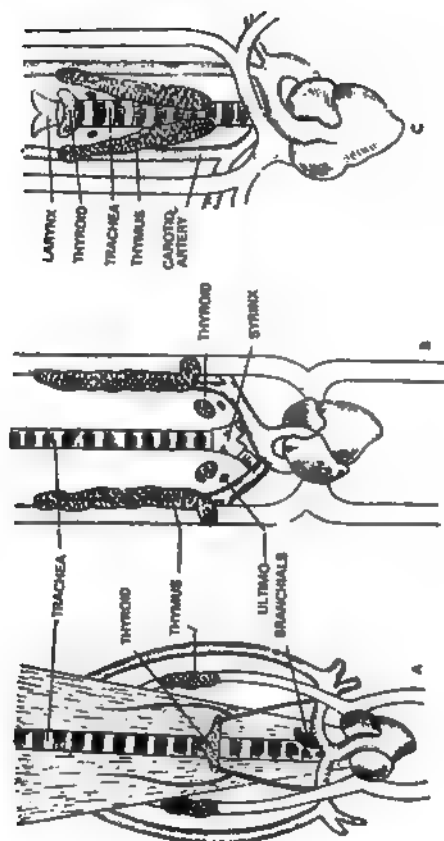


Fig. 9.5. Thyroid, parathyroid and ultimobranchial bodies in a vertebrate.

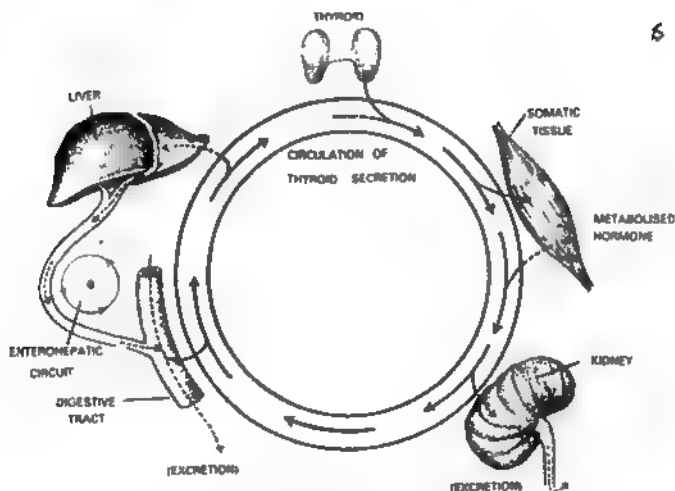


Fig. 9.6. Pattern of release, circulation, metabolism and excretion of thyroid hormones.

thyroids of a tadpole are removed (thyroidectomy) the tadpole does not metamorphose but grows to a giant size (Fig. 9.7). All tissues and systems are involved, and virtually all seem to be directly responsive to the thyroid hormone. Neoteny in certain larval salamanders and metamorphosis in non-amphibian vertebrates is also influenced by thyroid secretion.

Some people feel that in the absence of thyroxine animals do not grow well, but since there are other hormones which affect growth the role of thyroid hormone may be merely to create the climate in which true growth factors appear. It has been pointed out earlier that tadpoles may become giants in the absence of thyroid hormone (Fig. 9.7). Thus the target of thyroxine is the endoskeleton. In rats, from which thyroids have been removed bone growth like body weight is arrested while the histological structure of the bones remains of the youthful type. Human children with deficient thyroid apparatus become ill-developed individuals called **cretins** (Fig. 9.8). They have imperfect physical and mental development. The skeleton is not formed perfectly, remains infantile even in the adult stage. Mental growth is retarded and the patient becomes completely imbecile. Brown, Bronstein and Kraines (1939) showed that thyroid feeding of cretins increases mental activity and alertness.

The growth and eruption of teeth are clearly under thyroid control in various mammalian species. In hypothyroid children (cretins) the eruption of tooth both deciduous and permanent teeth is greatly delayed. For example it has been reported that a cretin almost 12 years old had a dental age of 5 years. The growth of the horns of deer can be greatly accelerated by thyroxine injections, other hormonal factors are also normally involved.

Recent authors have concluded that nervous function at all levels is influenced by thyroid, spontaneous electrical activity, threshold of sensitivity to a variety of stimuli, reflex time, motor behaviour. Furthermore thyroid regulation of neural activity is found in all major vertebrate groups. In cat, rabbit, dog and guinea pigs it has been shown that thyroid treatment causes increased spontaneous bioelectric activity of brain, increased excitability of brain (decrease of reaction time), increased respiration

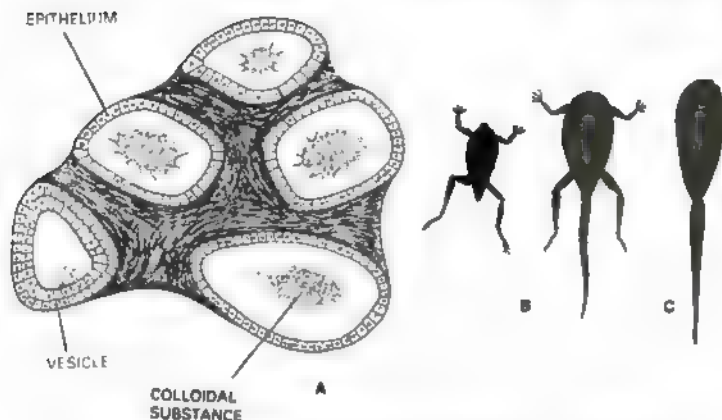


Fig. 9.7. A. cross-section through thyroid of frog. B. tadpole fed on thyroid undergoes metamorphosis. C. tadpole of the same age without thyroid feeding.

and mineral metabolism in brain, lowered threshold of excitability of certain reflexes (ear twitch). In rat removal of thyroid results in reduced spontaneous motor activity and maze-learning ability.

Thyroid hormone influences other physiologic activities: (i) Thyroid stimulates motor activity in the stomach and intestine, thus accelerating the movement of food through the gut. (ii) Thyroxine increases the rate of absorption of glucose, galactose, oleic acid and vitamin A from the intestine. (iii) Thyroxine or the hyperthyroid state causes an increased loss of water in urine (diuresis), thyroidectomy (removal of thyroid) or hypothyroidism results in a decreased urine volume, (iv) Thyroxine causes a loss of interstitial fluid from the skin and muscles, but an increase in water in the liver and blood, (v) Thyroxine controls oxygen consumption in man (this function has been repeatedly confirmed in all birds and mammals). Because of this the thyroid has been described as "a governor of metabolism" or a "thermostat".

The deficiency of thyroid secretion causes **myxoedema** in the adult. The symptoms of the disease include overgrowth of connective tissue or fat, loss of hair, weak muscular development, the skin becomes rough, peculiar swollen spots appear on the body, impoverished blood, deficient sexuality, lowered metabolism, nervous depression and frequently impaired mentality. This condition may be relieved or removed entirely by the proper administration of thyroxine.

Pathological overgrowth of thyroid results in a condition called common **goitre**, an enlargement of the thyroid due to deficiency of iodine. The overgrowth is enormous, the gland may weigh hundred times its normal weight. The follicles contain very little of the colloidal substance and the epithelial cells are enormously grown. In another condition the colloidal substance increases and the follicles become crammed with it. This is called the **colloidal goitre** (Fig. 9.8 B).

Overactivity of the thyroid gland results in **Grave's disease** or **exophthalmic goitre**, in which the patient becomes extremely nervous and thin exhibiting characteristically protruding eye-balls (hence **exophthalmic**). The symptoms disappear on the administration of thyroxine.

Parathyroid Gland. It was in 1880 that Sandstrom discovered parathyroid glands (Fig. 9.10) as anatomic entities. They were, therefore, known as **Sandstrom's glands** for a long time. The name parathyroid was given to them much later because they are located in close association with the thyroids in mammals. In lower vertebrates they

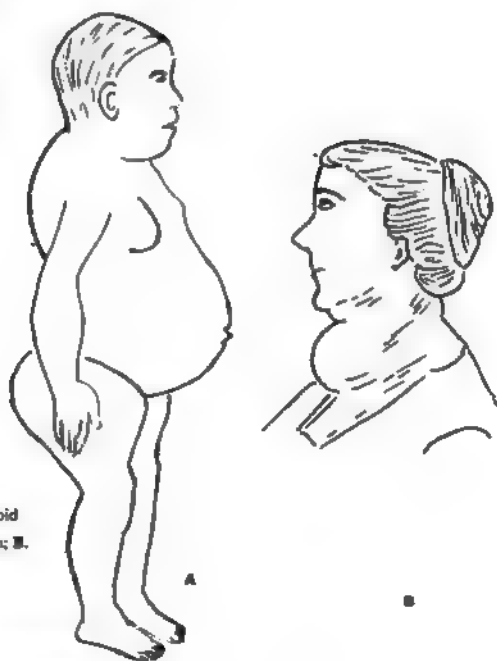


Fig. 9.8. Diseases caused by thyroid inactivity or deficiency. A. cretin; B. Goitre.

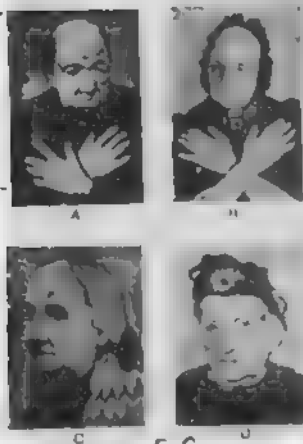


Fig. 9.9. Myxoedema caused by thyroid deficiency. A. an old patient; B. after five week's treatment, C. after 15 months treatment; D. after 30 years.

are referred to as epithelial bodies as they arise from the walls of the pharynx in the region of the gill pouches and are epithelial in the beginning. They become glandular only afterwards. Thymus glands and ultimobranchials also arise from the walls of the pharynx as epithelial structures.

Gley (1891) and Vassale and Generali (1896) worked on rabbits, dogs and cats and showed that the lethal effect followed by removal of thyroids was due to removal of parathyroids and not thyroids. The real endocrine nature of parathyroids was shown by Collip in 1925 who obtained active extract from the parathyroid of cattle and named it *parathormone*. The researches that followed have shown that parathormone acts upon bone and renal function in regulating the calcium and phosphate in blood and may even have other centres of activities.

The parathyroids are well enclosed in capsules (encapsulated) and made up of branching cords of cells separated by a network of capillaries or sinusoids. In the reptiles and amphibians the glandular parenchyma is more compact and seemingly less vascular. In man and other species two types of cells are recognised roughly cuboidal nongranular cells without any outstanding cytoplasmic characteristics (called the chief cells by some); and some cells having an eosinophilic cytoplasm with pyknotic nuclei (called oxyphil cells). In the frog there seem to be only one type of cells — elongated and arranged in whorls. Electron micrographs of parathyroids of mammals show that the nuclear membrane contains many pores (discontinuities). The cytoplasm of both chief and oxyphil cells in monkeys contains juxtanuclear bodies (made of stacks of parallel endoplasmic reticular plates). It is likely that they may be centres of synthetic activity in the cell. The cytoplasm of oxyphil cells is extremely rich in mitochondria.

Although parathyroid extracts were made available in 1925 the parathyroid hormone has not yet been isolated in its natural form. The biologically active substances extracted from parathyroid tissues are polypeptides destroyed by proteolytic enzymes (thus, ineffective by mouth). It is very remarkable that chemical properties of pure parathormone isolated from bovine parathyroids differ.

Function If the parathyroids are removed the animal becomes restless and is easily excited. Muscle tonus and the frequency of involuntary twitches increase, periodic spasmodic contractions of muscle groups makes the body posture unnatural and the gait uncertain. The animal soon develops parathyroid tetany. The tetanic fits become progressively more frequent. The animal ultimately dies. It is now known for certain that all parts of the nervous system (both voluntary and autonomic) show signs of hyper-irritability. The symptoms may be corrected by supplying exogenous calcium by mouth or by injection. If the level of calcium in the plasma is reduced by dietary restriction or by any other cause symptoms similar to parathyroid tetany are produced.

It is evident from this that the chief function of the parathyroid hormone is to regulate the quantity of calcium in blood plasma. As the level of the blood calcium falls the phosphate concentration rises. Injection of parathormone elicits a rise in blood calcium and a drop in phosphate concentration (a sharp increase in phosphorus level in urine). Hyperactivity of parathyroid destroys osteocytes and osteoblasts in the bone, removes calcium from the bone and increases it in the blood and urine. Often the bones become weak, bend or become brittle and cause various bone deformities. Parathormone treatment is followed by an increase in phosphate excretion which in mammals may be as much as twenty to forty times the normal rate. Calcium excretion also increases after a brief decrease. Parathyroidectomy (removal of parathyroids) has the opposite effect decreasing the excretion of both calcium and phosphorus.

Thymus. The thymus glands arise from the ventral region of the gill-pouches and has a multiple origin. Although present in all vertebrates they remain epithelial in fishes while in higher forms they become lymphoid and highly vascular. The different embryonic elements of the thymus frequently fuse together to form continuous masses of tissues on either side of the neck.

In the frog they lie behind the tympanum (Fig. 9.11), in *Proteus* behind the gills under the skin and so also in urodeles and *Gymnophiona*. In lizards they lie behind the tympanic drum ventral to the jugular, on each side. In lizards the thymus consists of two bodies, in snakes three bodies on each side, the middle one lying between the common carotids and the other two laterally to the carotid, in front of the heart.

In birds the thymus is a long, slender, lobulated structure running from the base of the skull to a little distance in front of the heart. In mammals the thymus has two separate parts, one lying inside the thorax in relation to the anterior pericardial wall and the other in the neck region. In man it reaches its maximum size at puberty although its greatest relative size is attained much earlier in infancy.

There are some who doubt whether or not the thymus is an endocrine organ. Hoskin says, "In all probability the organ is of significance in the physiological and pathological processes, merely by virtue of its lymphoid character." According to others there is slight evidence that it has an internal secretion. It decreases in size with age and becomes rudimentary at puberty. It is supposed to hasten the onset of sexual maturity. If removed from the young animals development of reproductive system is delayed.

Ultimobranchials. These are most posterior of the series of pharyngeal derivatives and are suspected of endocrine activities. They arise behind the fifth pair of gill-pouches. Only the left is developed in lizards and their occurrence in birds and mammals is doubtful. Their exact function is not known.

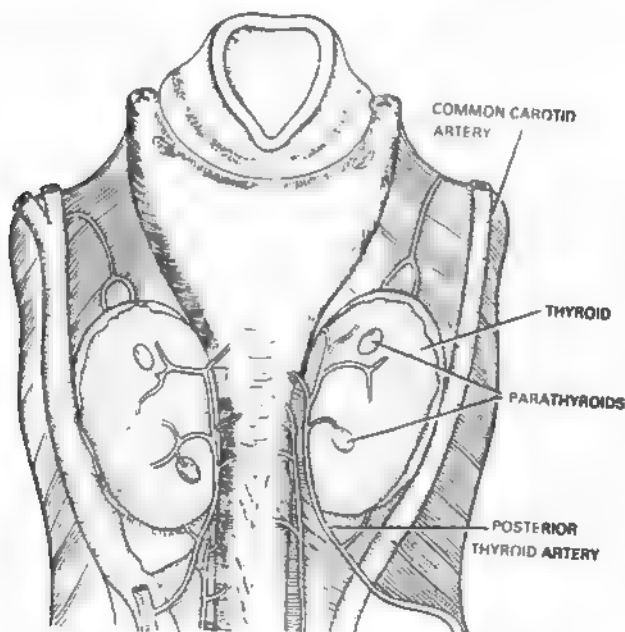


Fig. 9.10. Position of parathyroids in a child.

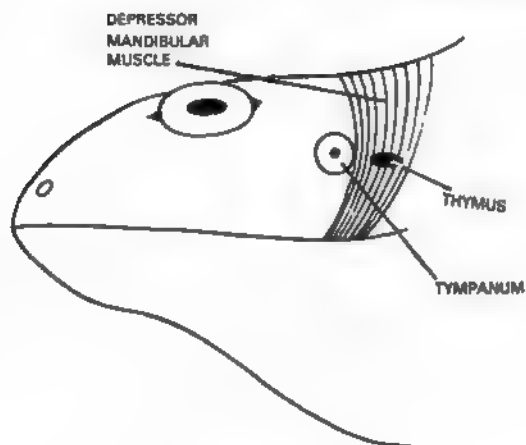


Fig. 9.11. Position of Thymus in frog.

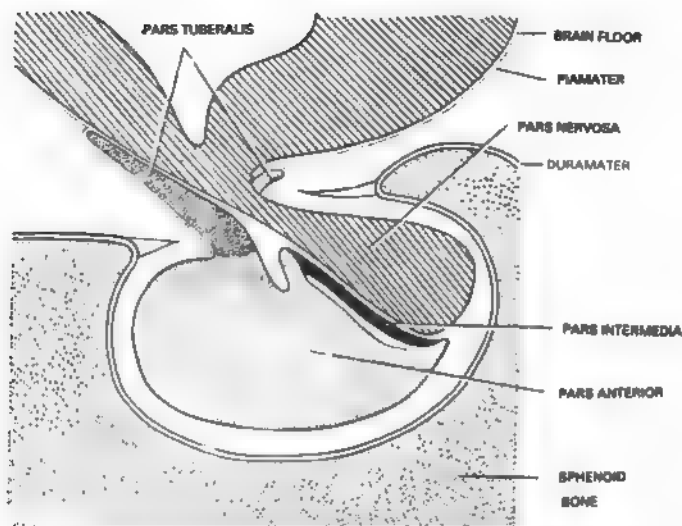


Fig. 9.12. A portion of the diagrammatic sagittal section of the skull through the region of hypophysis (after Atwell).

(ii) **Thyrotropic hormone** or **thyrotrophin** or **thyroid stimulating hormone (TSH)** is secreted by basophil cells and controls the growth and activity of the thyroid gland. In hypopituitarism, development of thyroid is retarded and a condition of thyroid hormone deficiency occurs. In hyperpituitarism thyroid often becomes hyperactive.

(iii) **Adrenocorticotrophic hormone (ACTH)** or **adrenotropic hormone** or **corticotrophin** is secreted by the basophil cells and controls the growth and secretion of adrenal cortex. The influence of anterior pituitary on carbohydrate metabolism may be due to the effect of this hormone through adrenal cortex. In hyperpituitarism adrenal cortex atrophies. Similarly, on hypopituitarism it degenerates or fails to develop. Tumours of the basophil cells (**Cushing's disease**) causes enlargement (even tumours) of adrenal cortex.

(iv & v) **Gonadotropic hormones** or **gonadotrophins**. The basophil cells secrete gonadotrophins which control the growth and activity of the gonads and indirectly all the other processes connected with it (*i.e.* growth of sex organs, secondary sex characters, and in the females the menstrual cycle, etc.). There are three gonadotrophins: (a) **Follicle stimulating hormone (FSH)**, (b) **Luteinising hormone (LH)**, or **Interstitial cell stimulating hormone (ICSH)**, and (c) **Lactogenic hormone** or **mammotrophic hormone (MH)**, or **Luteotropic hormone (LTH)** or **Prolactin**. Of these FSH acts both on male and female gametes (**Gametokinetic factor**). In females it increases the number and size of Graafian follicle and in males it stimulates spermatogenesis. LH is responsible for the appearance, growth and persistence of corpus luteum and stimulates the secretion of progesterone in females, while in males it stimulates the interstitial cells of the testes to secrete testosterone. LTH helps in the secretion of milk and in the secretory activity of the corpus luteum.

(vi) **Lactogenic hormone (LTH)** Or **prolactin**. It is secreted by eosinophil cells and controls the activity of mammary glands.

Intermediate Lobe. The intermediate lobe is a thin strip of tissue separated from the anterior lobe by the interglandular cleft. It secretes a hormone called **intermedin melanophore-stimulating hormone (MSH)**, which in the amphibia and fishes causes expansion of the pigment bearing cells (melanophores) of the skin. The skin colour thus becomes darker. Temporary darkening of the skin takes place in human beings on administration of MSH.

Neurohypophysis. Five functions have been attributed to the hormones of the neurohypophysis: (a) increase in blood pressure, (b) contraction of uterine muscles, (c) ejection of milk from mammary gland, (d) control of the amount (concentration) of water in the body fluids, and (e) stimulation of secretion of certain adeno-hypophyseal hormones. The first three of these act upon contractile tissue, the fourth involves the kidney causing to lose less fluid (antidiuresis) and excrete urine in more concentrated form. Stimulation of the adeno-hypophysis is clearly a local effect. Of those that act on contractile tissue are those that raise the blood pressure by constricting the blood vessels. **Vasopressin** (or **pitressin** and **betahypophamine**) is the hormone which raises blood pressure. The hormone which stimulates the contraction of the uterus is called **oxytocin** (also **pitocin** and **alpha-hypophamine**). Pituitrin oxytocin are widely used after parturition (child birth) when it is necessary to induce a sufficiently vigorous contraction of the uterus in order to expel the placenta and stop the uterine haemorrhage. The hormone which influences the excretion of urine is called **antidiuretic hormone (ADH)**. It stimulates reabsorption of water from the primary urine when the latter passes down the renal tubules. Antidiuretic hormone and vasopressin are chemically identical. In action a smaller concentration of ADH exerts only antidiuretic effect and with higher concentration it acts on the blood vessels also.

Some writers on endocrinology have associated temperamental characteristics with over or under-activity of the pituitary gland. Even Napoleon has been "explained" as a **hyperpituitous** man, 'though he was almost a dwarf and ran to early fat'. Over-secretion of the growth hormone seems to be accompanied by intense living, courage,

initiative and forcefulness of character whereas, with the wanting of secretion there supervenes lassitude, timidity and failure.

Pineal Body. The pineal body or epiphysis is a small outpushing from the roof of the diencephalon. It is found in most vertebrates but is sometimes degenerate. In elasmobranchs it reaches the roof of the skull where there is a foramen for this gland. In *Myxine* and crocodiles it is absent. In mammals it appears as a pinkish pouch that is covered by an outgrowth of the cerebral lobes, and is much more gland-like than in lower animals. In man the pineal body is glandular in early life but after puberty decreases in size and the glandular tissue is replaced by fibrous tissue.

The pineal (epiphysis) has long been suspected of having an endocrine function. Earlier workers studied the chronic effects of removal and of administration of extracts and concluded that the epiphysis acted to some degree in opposition to the hypophysis especially in an anti-gonadotropic sense. The data supporting this conclusion are questionable, and the other data indicating a relation to somatic growth are not accepted today. Signs of secretory activity occur in at least some cells of the gland. Histologically the organ is complex structure being composed of ependymal, glial, neuronal and other elements.

According to Van de Kamer ependymal cells of the pineal are probably photosensitive. The anatomic relations of the pineal to the third eye of reptiles are suggestive (Fig. 9.15). This middle (parietal or parapineal) eye is present along with a true epiphysis and is located anterior to the paraphysis-epiphysis region. In most vertebrates an eye-like epiphyseal structure is lacking but part of the epiphyseal apparatus is so superficially located as to be exposed to light in small animals with a thin cranial roof. In fishes the epiphysis lies beneath a translucent area of the skull.

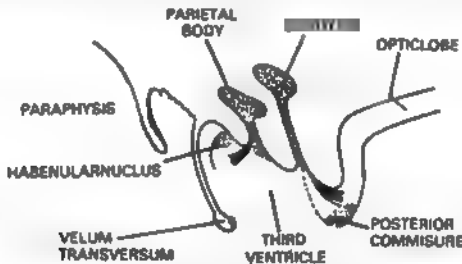


Fig. 9.15. Position of Pineal body.

Recent studies on the physiology of the structure have led to three suggestions :

(1) Lizards whose parietal eyes were removed were found to be less responsive to solar radiation (Stebbing and Eakin) perhaps the median eye acts as a kind of thermostat and inhibits motor activity and results in the conservation of metabolic reserves. Pflugfelder has found that the removal of epiphysis cause hypertrophy of thyroid.

(2) Farrell has reported that the diencephalic roof (epithalamus) is the source of a substance which stimulate, the zona glomerulosa of the adrenal cortex (adrenal glomerulo-trophin) and increases the secretion of aldosterone (an adrenal hormone).

(3) Lerner and his associates have extracted a highly powerful chromatophorotropic from pineals. This is a substance with low molecular weight and is called **melatonin**, a tryptaminé derivative, a minute quantity of which causes melanin concentration in melanophore and, hence, paling of frog skin.

Adrenal Glands. The adrenal gland is a compound structure with complex functions. In 1953 British Physician Addison described symptoms of a disease that is now called **Addison's disease**. It is now known that the disease is caused by

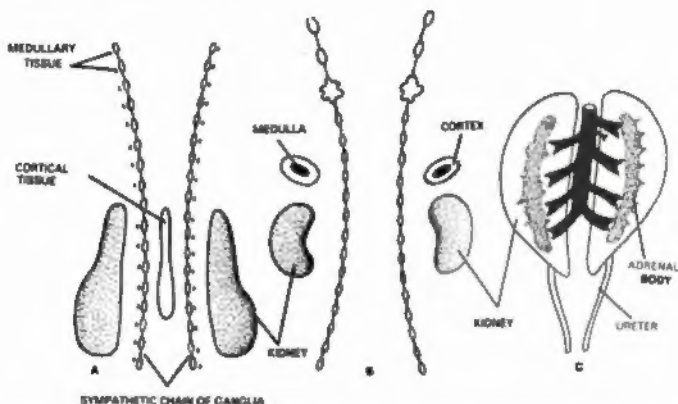


Fig. 9.16. Adrenal tissue in elasmobranch fish (A) and mammals (B) and C, formation of adrenal in frog.

insufficiency of the secretion of adrenal cortex and was associated by Addison himself with lesions in Adrenal gland. Brown-Sequard in 1856 attempted to study the effects of removal of the adrenals on animals. Later he concluded that adrenals were essential for life. In 1856 Vulpian distinguished cortical and medullary tissues.

They are complex structures made up of two parts, a **central medulla** and a surrounding zone the **cortex** (Fig. 9.16) derived from two sources. The medullary tissue is derived from a group of cells from which ganglia of the sympathetic nervous system arise. The cortex, on the other hand, arises from a mass of cells in close relation to those from which sex glands (testes and ovaries) are developed. The structures derived from two different sources remain separate in lower vertebrates, but they come in close association in higher vertebrates forming medulla and cortex of **adrenal bodies**. The name **adrenal** or **suprarenal** has been given to the gland because of their close anatomic and embryologic relations with the kidneys.

In cyclostomes and fishes (Fig. 9.16) the supra-renals and inter-renals remain separate and stretch throughout the trunk (and in cyclostomes even pass into the tail and the supra-renal into the head), in amphibia they represent an intermediate condition. In the frog, for instance, they appear as yellowish patches on the ventral surface of the kidney consisting of anastomosing strands of supra-renal and inter-renal tissue. In amniota they are more firmly combined to form a single pair of adrenals. In mammals they are clearly demarcated into cortex and medulla as mentioned above but not so in the reptile and birds. The two parts are embryologically, structurally and functionally different.

Histologically the adrenal cortex (Fig. 9.2) consists of polyhedral cells with well defined nuclei, typical mitochondria, Golgi apparatus and numerous doubly refractile lipid granules in the cytoplasm, called **sudanophil granules** as they stain easily with Sudan III solutions. The cells are arranged in three layers (i) **zona granulosa** outer layer with groups of columnar cells with their long axis parallel to surface. (ii) **Zona fasciculata** the middle wider layer containing larger polyhedral cells with pigment granules. The cells are arranged in radiating columns perpendicular to the surface. (iii) **zona reticularis** the inner layer made up of an irregular network of rows of cells containing lipid droplets (liposomes).

Zona glomerulosa secretes **aldosterone** while **zona fasciculata** and **zona reticularis** secrete **cortisol**, **corticosterone**, **sex hormones**, etc. **Zona fasciculata** is very rich in

Women who are the victims of cortical enlargement or tumour become obese and masculine in appearance, hair grow upon the face and chest and the disposition tends towards "mannishness". This condition is referred to as **virilism**. Lukens and Palmer have reported an excellent example of virilism. The female patient was normal till the age of six, when she had scarlet fever. A few months later it was noticed that her voice was becoming deep and hoarse, then hair appeared on her upper lip and by the time she was nine years old she had full beard, and her entire body was covered with hair. She had a masculine figure, great muscular strength, and was considered tall for her age. Psychologically she always remained distinctly feminine. She retained these features that kept on growing till the age of sixteen when she was examined thoroughly and it was discovered that she had a large tumour in the region of the right adrenal. She was operated upon and the tumour was removed with the result that she made complete recovery.

A similar case has been reported for an adult man, a father of one child, who became feminine at the age of 32, when his breasts began to enlarge, weight showed rapid fall, and some masculine features began to atrophy. At operation a large malignant tumour of the left adrenal was removed and, although the convalescence was protracted, after two months the patient began to gain weight and strength.

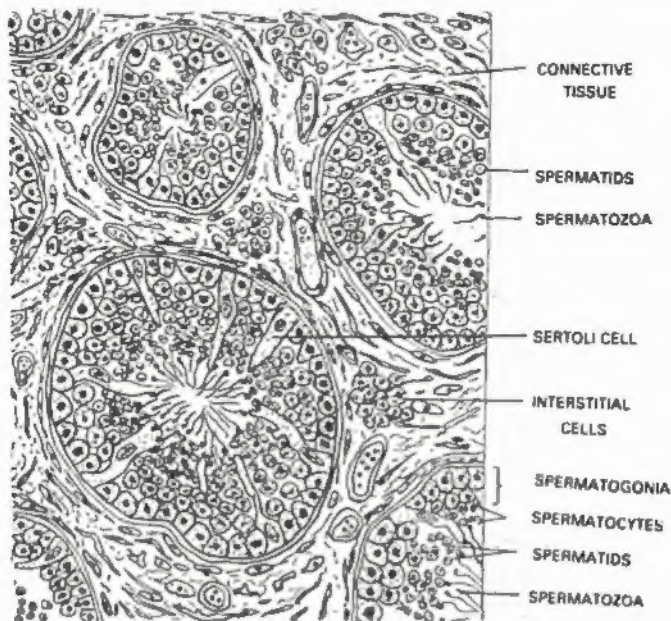


Fig. 9.20. Transverse section of testis of a vertebrate showing interstitial cells that secrete male hormone.

Gastrointestinal Hormones. The integration of digestive process is brought about by hormones formed in the glandular mucosa of the alimentary canal. The gastrointestinal hormones are released into the blood on the arrival of food. They then elicit a muscular response (as in the gall bladder) or glandular secretion (as in the



Fig. 9.21. Horns, example of secondary sexual characters

secondary sexual characters in other animals. To study the effects of the hormones released by the gonads usually the sex glands have to be removed (excised). This process is called **castration** in both sexes. Excision of the ovaries is called **oophorectomy** or **spaying**.

Testis. The interstitial cells of the testes produce hormone which is responsible for the development of secondary sexual characters (including the external genitalia). These characters include deep voice, muscular development, masculine contours and distribution of hair on the face and body. Removal of testes (**castration**) before puberty seriously interferes in the formation of these structures but removal after puberty has little or no effect. The testicular hormone consists of many related substances. **Androsterone** is an active agent. It has been found to induce the formation of comb in castrated male poultry. **Testosterone** is another that has been isolated from the testicular extracts. When the male chicken (cockere) is castrated the secondary sexual characters do not appear and sex instinct is suppressed. The castrated birds are known as **capons**, their body weight is greater than the body weight of the normal males of the same age. Castration of young stage prevents the development of antlers.

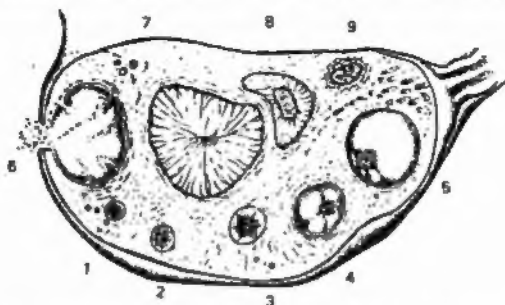


Fig. 9.22. Transverse section of ovary of a mammal showing the development of Graafian follicle. 1-5 Ovum develops from a simple layered follicle to mature graafian follicle. 6. Ovulation takes place. 7-9, corpus luteum is formed.

Ovaries. The sex organs in the female, like the male, mature at a fixed age, **puberty**. The reproductive period extends throughout the greater period of life of the animal. In the majority of the animals, the female will receive the male at a certain period or periods of the year. These mating seasons are called "heat" by the animal breeders and **oestrus** by the physiologists. The phase preceding oestrus is called **pro-oestrus**, that following **post-oestrus**.

The phenomena of the oestrus cycles are dependent upon hormones produced in the ovary. A hormone called **oestrin** or **theelin** is produced by the cells lining the

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ISBN : 0-85226-928-5

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